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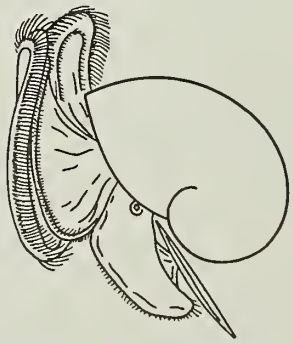

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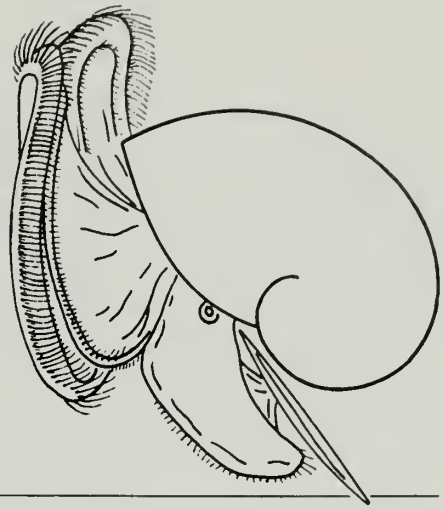

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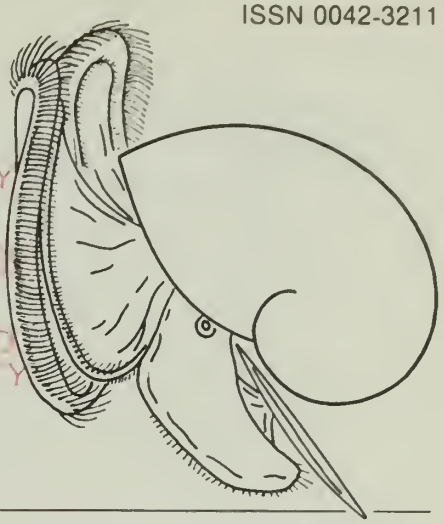

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Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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Temporal Patterns of Nudibranch Mollusk Activity on a Subtidal Hawaiian Reef

by

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Abstract. Differences in abundance and diversity of nudibranchs based on day and night sampling on the same shallow subtidal Hawaiian reef are documented. Species active during the day tend to be brightly colored and contrast with their surroundings, while those active at night are more likely to possess cryptic coloration. Abundance is greater during day sampling, but diversity is substantially greater at night.

INTRODUCTION

Nudibranchs are soft-bodied animals capable of secreting themselves in holes and cracks so effectively that they are often overlooked by even the most careful observer. Frequently, one or more nudibranchs completely invisible during a thorough external examination of a rock will suddenly appear after that rock is placed into an aquarium. This characteristic of nudibranchs could conceivably affect the results of nudibranch population studies such as that of NYBAKKEN (1978), who calculated diversity based upon numbers found by visual examination of rocks. If one or more species that typically hide in small cracks and holes experienced population fluctuations, it could have affected Nybakken's conclusions. Nybakken was aware of this possibility; he pointed out the difficulty of sampling some of the smaller, more cryptic species. Similarly, POTTS (1970) admitted that estimates of abundance during his study were low due to inaccessibility of some rock crevices.

The study arose from the observation that nudibranch species never or rarely observed during the day could be found easily at night. According to HARRIS (1973), ". . . in Hawaii . . . a number of species . . . are photonegative and nocturnal, but many more are active during the day." However, observations made during day and night scuba dives on a shallow subtidal reef off the island of Oahu, Hawaii, suggested that more species could be found at night than are typically found during the day. This study was undertaken to: (1) verify the observation that the sampled nudibranch assemblage differs depending on the time of day that sampling takes place, and (2) try to determine whether nocturnal nudibranch sampling would be a way to obtain a more accurate estimate of nudibranch populations.

METHODS

The location and characteristics of the sampling site are described in JOHNSON (1983). Briefly, the study reef is at Makua (21°32′50″N, 158°13′32″W) on the western shore of Oahu, Hawaii. The reef is on the southern face of a basaltic peninsula extending outward from shore. The site consists of a subtidal vertical cliff, 200 to 300 m in length and varying in depth from 2 to 6 m. The cliff forms a nearly complete circle, offering a gradient of exposure to wave action. The cliff face is pocketed with innumerable holes, caves, and ledges, most of which are thickly encrusted with sponges and other sessile organisms.

Preliminary sampling to determine major differences was done by timed swims along the study cliff, carefully examining the path for nudibranchs. A total of 52 h of timed-swim counting was done during the day and 34 h at night.

For a more direct comparison, 12 permanent and 25 randomly chosen m^2 quadrats were sampled. All quadrats were carefully and thoroughly searched for nudibranchs on each of six different sampling expeditions. The same 12 permanent quadrats were sampled on each expedition to the study site; these 12 quadrats were selected to be approximately equidistant around the study reef and were all ledges or small caves with high cover of sponges and other encrusting organisms (the most likely areas to find nudibranchs in Hawaii; see BERTSCH & JOHNSON, 1982). The 25 random quadrats were chosen anew on each of the six expeditions (see JOHNSON, 1983, for a description of how the quadrats were selected). For each expedition, the same permanent and random quadrats were sampled once during the day and again that night.

Within each quadrat, the number of nudibranchs of each species was noted, as well as the substrate beneath each individual and whether or not the nudibranch was feeding. Also, each species observed was judged to be cryptic or

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flamboyant based on how easy it was to see in its typical surroundings.

Note that this difference between cryptic and flamboyant is highly subjective and depends upon a number of factors. First, it assumes that observations are made during the day; in the dark, all species are cryptic. Second, substrate is important. A nudibranch highly cryptic on one substrate may be flamboyant on another. Third, depth may also be a factor. As colors fade with increasing depth, what is a flamboyant color pattern in shallow water may become a camouflaged pattern on the same substrate in deeper water. The decisions on cryptic or flamboyant in this paper are based solely upon how the nudibranch appeared in its usual habitat in the Makua site, which is shallow enough for all or most colors to be visible during the day.

Shannon-Wiener diversity indices (H) were calculated for both day and night samples using the formula:

$$H = -\sum_{i=1}^{s} p_i(\ln p_i)$$

where p_i is the proportion of the ith species and s is the number of species. Equitability (J), the "evenness" of the abundances of the various species, is defined as:

$$J = H/(\ln s)$$

T-tests were performed to determine whether the mean diversity differed between the day and night samples.

RESULTS

In 52 h of timed swims along the study reef during the day, 3081 nudibranchs representing 25 species were observed, yielding an average of 59.3 nudibranch individuals per search hour. In 34 h at night, 1898 nudibranchs spread over 44 species were observed, for an average of 55.8 per hour.

Table 1 shows the breakdown of species and abundances for all 222 quadrats sampled both day and night. In the day quadrats, 465 individuals of 17 species were counted; at night, the count totalled 407 individuals of 26 species. In the column labeled "Visibility," "flamboyant" indicates that the nudibranchs were easy to see in typical surroundings; "cryptic" means that they were difficult to see or hard to recognize as nudibranchs (even using a flashlight at night).

Table 2 summarizes the numbers of the five most common species found during the day and night quadrat sampling. Only two species are present on both lists. The other three species on each list show considerable disparity in abundances between day and night.

Shannon-Wiener indices and equitability statistics calculated for the day and night quadrat samples are compared in Table 3 for each of the six sampling expeditions. A t-test comparing mean diversity between day and night shows differences to be significant ($t = 6.1429 > 3.169 = t_{10,0.005}$). Mean equitability between day and night also differs significantly ($t = 4.3416 > 3.169 = t_{10,0.005}$).

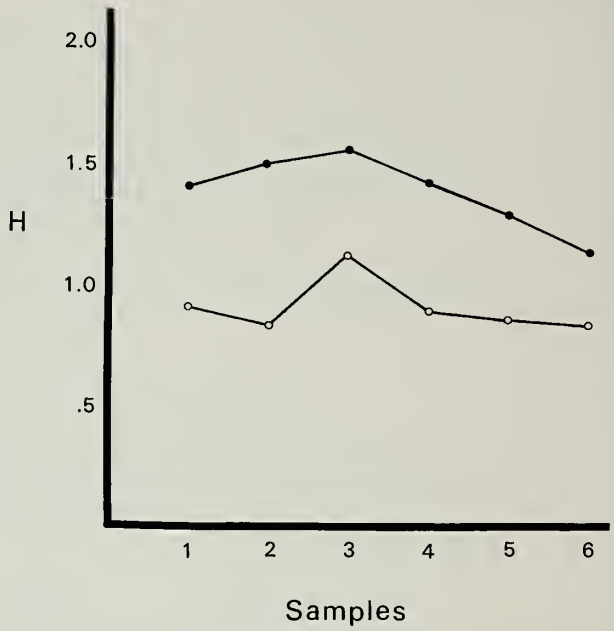

Figure 1

Diversity (H) of day (open circles) and night (closed circles) samples over the study period.

A merged count of nudibranchs was made using the larger of the day or night numbers counted for each species observed in the quadrats on a particular sampling expedition (*e.g.*, if 15 specimens of a species were counted during the day and 10 at night, the day figure was used; if more were found at night than during the day, the night figure was used). Shannon-Wiener and equitability statistics were also calculated for these merged samples (Table 3). Calculated diversity is greater for the merged samples than for either the night or day samples alone.

DISCUSSION

Abundances

Both timed-swim and quadrat counts reveal large differences in the species observed and their relative abundances. Although more species are observed at night, the overall number of nudibranchs counted is greater during the day. This is due primarily to the reduced numbers of the two most abundant species at night.

Glossodoris rufomarginata (Bergh, 1890) (=*Chromolaichma youngbleuthi* (Kay & Young, 1969) in JOHNSON, 1983), although by far the most abundant nudibranch at all times, is less frequently observed in the same quadrats at night than during the day. The animals' behavior explains this difference. During the day, specimens of this small (2–30 mm), brown-speckled nudibranch are nearly always observed preying upon a massive, dark gray to black sponge that lives in ledges along the cliff face (JOHNSON, 1983); 82.6% of the individuals observed during the day were on

Table 1

Nudibranchs observed in 222 1-m² quadrats along the Makua reef.

Species	Day		Night		Visibility
	Total no.	% of total	Total no.	% of total	
Glossodoris rufomarginata (Bergh, 1890)	334	71.83	264	64.86	flamboyant
Hypselodoris sp. 1[a]	82	17.63	10	2.46	flamboyant
Aldisa pikokai Bertsch & Johnson, 1982	0	0.00	34	8.35	cryptic
Halgerda terramtuentis Bertsch & Johnson, 1982	6	1.29	13	3.19	cryptic[b]
Sclerodoris paliensis Bertsch & Johnson, 1982	0	0.00	17	4.18	cryptic
Chromodoris sp. 1	0	0.00	13	3.19	cryptic
Chromodoris sp. 2[c]	4	0.86	7	1.72	flamboyant
Chromodoris vibrata (Pease, 1860)	7	1.51	3	0.74	flamboyant
Phidiana indica (Bergh, 1896)	4	0.86	5	1.23	flamboyant
Hypselodoris sp. 2[d]	8	1.72	0	0.00	flamboyant
Hexabranchus sanguineus (Rüppell & Leuckart, 1828)	1	0.22	7	1.72	flamboyant
Hypselodoris sp. 3	5	1.07	2	0.49	flamboyant
Chromodoris albopustulosa (Pease, 1860)	3	0.65	3	0.74	flamboyant
Phyllidia varicosa Lamarck, 1801	2	0.43	4	0.98	flamboyant
Phestilla melanobrachia Bergh, 1874	2	0.43	4	0.98	cryptic
Chromodoris sp. 3[e]	1	0.22	3	0.74	flamboyant
Chromodoris albopunctata (Garrett, 1879)	1	0.22	2	0.49	flamboyant
Jorunna alisonae Marcus, 1976	0	0.00	3	0.74	cryptic
Plocamopherus sp.[f]	0	0.00	3	0.74	cryptic
Pteraeolidia ianthina (Angas, 1864)	2	0.43	1	0.25	flamboyant
Chromodoris sp. 4	2	0.43	0	0.00	flamboyant
Phyllidia pustulosa Cuvier, 1804	1	0.22	1	0.25	flamboyant
Dendrodoris sp. aff. *rubra* (Collingwood, 1881)	0	0.00	2	0.25	flamboyant
Okenia sp.	0	0.00	2	0.49	cryptic
Chromodoris aspersa (Gould, 1852)	0	0.00	1	0.25	flamboyant
Sclerodoris sp.[g]	0	0.00	1	0.25	cryptic
Phyllidia sp. 2[h]	0	0.00	1	0.25	flamboyant
Bornella sp.	0	0.00	1	0.25	cryptic

[a] "Locust" in BERTSCH & JOHNSON, 1981 (B & J).
[b] Could be considered cryptic or flamboyant.
[c] *Chromodoris albonotata* in B & J.
[d] *Hypselodoris lineata* in B & J.
[e] "Snowflake" in B & J.
[f] *Plocamopherus tilesii* in B & J.
[g] *Halgerda rubra* in KAY & YOUNG, 1969.
[h] "Blue-black *Phyllidia*" in B & J.

the rather smooth-surfaced sponge, against which they were conspicuous. At night, individuals of this species had a tendency to move off the sponge. Only 43.2% of the *G. rufomarginata* observed at night were on the prey sponge; the rest were usually on the hard, irregularly shaped reef surfaces near the sponge colonies. (Percentages on prey sponges were obtained from the quadrat data only.) *Glossodoris rufomarginata* individuals observed at night were generally contracted and quiescent, rarely crawling, and never actively feeding. These observations suggest that *G. rufomarginata* is a day-active species. The numbers observed at night, however, indicate that individuals of this species do not effectively hide when they are not active.

The second most abundant species, *Hypselodoris* sp. 1 (=chromodorid 1 in JOHNSON, 1983), is also active during the day. Contrasting with *Glossodoris rufomarginata*, however, *Hypselodoris* sp. 1 hides very well at night.

During the day, *Hypselodoris* sp. 1, a small (2–15 mm) nudibranch, is commonly observed actively crawling or feeding, often in aggregations, on a bright yellow sponge. Occasionally, aggregations of 30 or more individuals totally devour a colony of the sponge down to the calcareous or basaltic substrate (JOHNSON, 1983). This process of decimating an entire sponge colony often takes weeks; yet night observations of a colony being preyed upon always reveal no nudibranchs. To determine where the nudibranchs go after dark, one aggregation of 34 individuals on a sponge colony was watched from late afternoon into early evening. About 1½ h before sunset, as the light level on the reef was diminishing, one individual of *Hypselodoris* sp. 1 crawled about 10 cm from the chunk of sponge it had been eating and disappeared into a small crack in the reef. (This crack was located in a bare patch of reef that previously had been covered by the yellow prey sponge,

Table 2

Comparison of the five most abundant diurnal and nocturnal nudibranchs in the 222 1-m² quadrats.

Day		Night	
Species	No.	Species	No.
Glossodoris rufomarginata	334	*Glossodoris rufomarginata*	264
Hypselodoris sp. 1	82	*Aldisa pikokai*	34
Hypselodoris sp. 2	8	*Sclerodoris paliensis*	17
Chromodoris vibrata	7	*Chromodoris* sp. 1	13
Halgerda terramtuentis	6	*Halgerda terramtuentis*	13

but which had been grazed clean.) Others followed along the same track at irregular intervals, possibly following a mucous trail. By sunset, the few nudibranchs not already in the crack were actively moving. By dark, not a single specimen was visible. All had vanished into the same crack in the reef. When the sponge colony was next examined, at approximately 11 A.M. the next morning, 32 *Hypselodoris* sp. 1 individuals could be counted on and in the sponge.

The behavior of moving away from the prey sponge and into a hole in the reef was later observed during several other dusk observations.

Only 10 individuals of *Hypselodoris* sp. 1 were observed in the quadrats at night as opposed to 82 during the day. Of the 10 observed at night, nine were packed together in a small hole in the reef next to a sponge colony that earlier that day was observed being preyed upon by 29 specimens of *Hypselodoris* sp. 1.

Species active exclusively at night include *Chromodoris* sp. 1, *Aldisa pikokai* Bertsch & Johnson, 1982, and *Sclerodoris paliensis* Bertsch & Johnson, 1982. No individuals of these species were observed during day sampling; yet, these three were among the most frequently observed species at night.

Predation and Warning Coloration

Why is there such a disjunct pattern of day and night activity among nudibranchs on this reef? Two possible answers are ease of feeding and predator avoidance. The former can probably be discounted. Of the 28 species in Table 1, 23 are sponge predators, two eat hydroids, one preys upon hard corals in the genus *Tubastraea,* and at least one eats bryozoans (feeding data from KAY & YOUNG, 1969; BLOOM, 1976; BERTSCH & JOHNSON, 1981; JOHNSON, 1983; and personal observations). All these prey items are sessile and attached to the substrate; they should be no easier to "catch" during the day or night. It is possible that each nudibranch species is most active when its prey's defenses are at a minimum (*e.g.,* if production of sponge toxins varies between day and night). This possibility was not tested but does not seem likely.

The question of predator avoidance is more difficult to assess. Nudibranchs may avoid predation by being distasteful or poisonous, or by being hard to find. The nudibranchs in the Makua study site range into both extremes of visibility; there are brilliantly colored species that contrast sharply with their surroundings, and there are extremely cryptic species that are very difficult to see.

The presence of brilliantly colored species raises the possibility of warning coloration. Warning coloration has been suggested many times to explain nudibranch coloration (*e.g.,* GARSTANG, 1890). However, as THOMPSON (1960) correctly pointed out, it is dangerous to assume that warning coloration exists without being able to show that potential predators hunting by vision avoid the color pattern in question, and that the prey has some characteristic making them unpalatable. In THOMPSON'S (1960) laboratory experiments, certain fish species refused all healthy individuals of cryptic and non-cryptic opisthobranchs, but readily accepted damaged specimens, suggesting that coloration is not important in deterring predators.

Laboratory experiments, however, cannot show that fish or other predators never eat opisthobranchs in nature, and natural observations are difficult to make. Except in certain cases (such as an animal grazing upon a sessile organism), acts of predation in the marine environment are rarely observed; the amount of time a predator spends actually consuming a prey is small compared to the total time hunting or doing other things. An act of predation upon a nudibranch, if it occurs, is likely to be of very short duration and to leave no tell-tale evidence (*e.g.,* the empty or crushed shell of a prosobranch gastropod). It may take many hours of observation to encounter predation upon a nudibranch even once, especially if the potentially cryptic coloration or toxic defenses are effective.

Despite the difficulty of observing natural predation, I have witnessed what appeared to be predation upon nudibranchs in the Makua site twice, both at night. In one case, a spiny lobster, *Panulirus marginatus* (Quoy & Gaimard, 1825), attacked and consumed an apparently healthy *Hexabranchus sanguineus* (Rüppell & Leuckart, 1828). In the other, a portunid crab, *Charybdis orientalis* Dana, 1852, was observed eating a *Dendrodoris elongata* Baba, 1936. In the latter example, the attack of the predator was not observed; only the fact that the crab was eating the nudibranch. The nudibranch could have been dead, dying, or damaged before the crab began to eat it. (*Dendrodoris*

Table 3

Comparison of the Shannon-Wiener Index (H) and Equitability (J) between day, night, and "merged" quadrat samples.

	Day		Night		Merged	
Sample	H	J	H	J	H	J
1	0.9169	0.4712	1.4001	0.5459	1.5532	0.5602
2	0.8465	0.4350	1.5171	0.5749	1.6332	0.5891
3	1.1491	0.4990	1.5597	0.6504	1.6878	0.6233
4	0.9004	0.4330	1.4293	0.5752	1.5574	0.5751
5	0.8668	0.3945	1.2970	0.5220	1.5294	0.5516
6	0.8325	0.4646	1.1557	0.5019	1.3895	0.5265

elongata is a nocturnal species observed several times on the timed swims, but was never present in any of the sampled quadrats.)

There is evidence that visual predators attack healthy nudibranchs in other areas. In Micronesia (Enewetak Atoll, Marshall Islands), labrids of the genus *Thalassoma* approached to within 25 cm of my face mask to decimate a group of the cryptic *Phestilla lugubris* (Bergh, 1890) on the underside of an overturned rock. Similarly, TODD (1981) reported labrids voraciously feeding upon small nudibranchs and sacoglossans on the exposed undersurfaces of rocks.

These observations suggest that predation can and does occur on nudibranchs in nature; only the extent is unknown. Given that some predation occurs, the present study provides circumstantial evidence that warning coloration does play a part. If it is assumed that diurnal species are those more than twice as likely to be found during the day and nocturnal species more than twice as likely to be found at night, Table 1 indicates that colorful species such as chromodorids and phyllidiids tend to be diurnal, while cryptic species are more likely to be nocturnal.

Several species require further comment. Although *Glossodoris rufomarginata* is not twice as likely to be found during the day than at night, it was already shown to be day active. Extensive observations of all the different species of *Phyllidia* and many species in the family Chromodoridiidae indicate that these species may be found with equal ease either day or night. Finally, *Halgerda terramtuentis* may be either cryptic or flamboyant on typical substrates. Against yellow sponge or multicolored sponge backgrounds, *H. terramtuentis* is cryptic; on hard reef coated with purplish encrusting algae, it contrasts sharply and is easy to see.

Some species are known to possess anti-predator defenses. Secretions from *Phyllidia varicosa* Lamarck, 1801, are known to kill other animals (JOHANNES, 1963), and the toxic compounds found in *P. varicosa* occur in other species of *Phyllidia* as well (G. Schulte, personal communication). *Dendrodoris tuberculosa* (Quoy & Gaimard, 1832), a species found in the day timed swims but not in the quadrats, produces secretions irritating to human eyes (BERTSCH & JOHNSON, 1981). *Pteraeolidia ianthina* (Angas, 1864) feeds upon hydroids and stores rather potent nematocysts in their ceratal tips (BERTSCH & JOHNSON, 1981). Chromodorids in general are characterized by large glands along the mantle margin (EDMUNDS, 1981; RUDMAN, 1984) which may be defensive in nature.

Observations in other areas indicate that predators avoid certain nudibranchs. At Magic Island, Oahu, Hawaii, many individuals of the flamboyantly colored *Risbecia imperialis* (Pease, 1860) (=*Chromodoris godeffroyana* (Bergh, 1879) in JOHNSON & BERTSCH, 1979, and BERTSCH & JOHNSON, 1981) possess healed wounds that appear to be bite marks (personal observation). If these highly conspicuous, always exposed nudibranchs were palatable, it is likely that fewer would be bitten only once and left to heal. At Enewetak, the same individuals of *Thalassoma* that readily preyed upon *Phestilla lugubris* (described above) ignored a brightly colored *Chromodoris fidelis* (Kelaart, 1858) under the same rock.

Many nudibranchs are known to contain organic compounds that may be toxic to predators (*e.g.*, SCHULTE *et al.*, 1980; SCHULTE & SCHEUER, 1982; FAULKNER & GHISELIN, 1983; OKUDA & SCHEUER, 1985). Examining the literature on chemical studies suggests that most experiments have been performed on those that fall into the flamboyant category rather than on those that are more cryptic.

While most chromodorids are less common (or at least, not significantly more common) at night than during the day, one undescribed chromodorid species encountered in this study, *Chromodoris* sp. 1, is strictly nocturnal. This nocturnal species possesses uncharacteristically (for a chromodorid) dull coloration, with translucent grayish spots on a white background and a faint yellow tinge to the margin. From a distance, the nudibranch resembles one of the reef's common sponges, which is oval and white with faint spots.

Some of the other abundant nocturnal species are extremely cryptic, even when illuminated with a bright light. *Aldisa pikokai* and *Sclerodoris paliensis*, while bright red and yellow respectively, strongly resemble clumps of sponge and are difficult to recognize as nudibranchs (see color photographs of *Aldisa* sp. and *Sclerodoris* sp. in BERTSCH & JOHNSON, 1981:44–45). At least to humans, these and

several other nocturnal species are extremely cryptic. If a species must hide from view (either by cryptic coloration, nocturnal habits, or both), it seems reasonable that it might not possess chemical defenses.

The next logical step would be to try to locate predators that would eat these nocturnal species and also to examine more of the cryptic species for unusual organic compounds that affect potential predators. Additionally, these organic compounds must be shown to protect the nudibranchs from predation; as SCHULTE & SCHEUER (1982) point out, it has not been demonstrated in most cases that organic compounds found in nudibranchs do in fact repel predators.

A lack of chemical defenses in the cryptic or nocturnal species contrasting with the presence of such defenses in brightly colored diurnal species would add more evidence both for the existence of warning coloration in nudibranchs and for predator avoidance as a major reason for the difference between day and night activity.

Diversity

NYBAKKEN (1978) reviewed some of the controversy regarding which diversity index is preferable. He chose the Brillouin index because of his not completely random sampling data, and because he was interested only in local diversity in a particular area and its variation. He also computed the Shannon-Wiener index for comparison and found that the two indices, at least for his data, were closely correlated. In the present study, the Shannon-Wiener index was used for ease of calculation with the rather large numbers involved. Whether or not the index gives a "true" estimate of diversity, it is certainly adequate for comparing the relative diversity of day and night samples.

Because of the larger numbers, it is tempting to use the data from the timed swims for the diversity calculations. However, the differences in total search times between night and day, and the biases inherent in a haphazard searching technique, make these data unacceptable for such statistical analyses. Using the haphazard sampling technique represented by the timed swims, one is far more likely to miss a 4-mm long, white *Okenia* sp. than a 200-mm, bright red *Hexabranchus sanguineus*. Careful searching of limited quadrats yields a far more realistic estimate of nudibranch proportions.

The greater diversity and equitability observed on the Makua reef at night substantiates the observation that there is a significant amount of nocturnal activity in addition to what is observed during the day. This points out clearly that, at least for this reef, daytime sampling is insufficient for determining the numbers and proportions of the different nudibranch species present. Because of day-active species that hide at night (such as *Hypselodoris* sp. 1), nocturnal sampling is also inadequate. A more realistic estimate of abundances might be obtained by sampling both day and night, and using the larger of the two counts obtained for each species (*e.g.*, the column labeled "Merged" in Table 3).

It might be argued that combining the different samples to produce the merged statistics is invalid. However, because of the differences in activity, it could equally be argued that the day or night counts alone produce diversity values that are at best unacceptable and at worst meaningless. While not an exact representation of the true diversity, the merged value is based on a better minimum abundance of each species present and should therefore be a closer estimate of the actual diversity.

Comparison of the results of this study with similar observations from other areas is useful. Personal observations at Enewetak, Marshall Islands, west central Pacific, suggest that the day vs. night difference in activity is not nearly as pronounced as on the Makua reef. Nearly all species of nudibranchs at Enewetak tend to hide during the day, perhaps owing to the effects of higher levels of solar radiation on prey sponges (see JOKIEL, 1980, and the discussion of the "inside-out phenomenon" in BERTSCH & JOHNSON, 1982). Examination of temporal differences in activity by different species might be most interesting in a place such as southern California, where numerous subtidal nudibranch species and their prey are found completely exposed in the daytime.

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Zonation and Behavioral Patterns of the Intertidal Gastropods *Nodilittorina* (*Tectininus*) *antoni* (Philippi, 1846) and *Nerita versicolor* Gmelin, 1791, in the Bahamas

by

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Abstract. The herbivorous tropical gastropods *Nerita versicolor* Gmelin, 1791, and *Nodilittorina* (*Tectininus*) *antoni* (Philippi, 1846) have an overlapping vertical distribution on intertidal, rocky shores of the Bahamas. Zonation and behavioral patterns of these mollusks were examined in relation to the tidal gradient, microhabitat characteristics, and the occurrence of the other snail species. Densities of the two gastropods at low tide were negatively correlated ($P < 0.05$) at sites etched with numerous, small pits. At these sites, the smaller snail, *Nodilittorina antoni,* predominated in the high zone; the larger *Nerita versicolor* was rare in high zones at all sites except one that lacked such small pits. *Nodilittorina antoni* rarely occurred below the high-mid zone at any sites. Observed distribution patterns were re-established following transplant of marked snails outside their respective zones, both in the presence and absence of the other species. Both gastropods, particularly *Nodilittorina antoni,* were most abundant in crevices or pits during daytime low tides, a period of inactivity. Continual emergence and submergence experiments indicated that vertical ranges of both species were well within physiological tolerances. Gut analyses indicated that the gastropods had a similar diet of cyanobacteria, which predominated throughout their vertical range. The shore-level gradients of snail size and density, as well as behavioral patterns, suggest an active response to microhabitat characteristics and, possibly, predation pressure.

INTRODUCTION

Experimental work on rocky shores has revealed the importance of both physical and biotic processes in regulating density and distribution of intertidal gastropod populations. Desiccation and heat stress, particularly critical during low tides in tropical environments (MOORE, 1972), affect snail behavior, resulting in limited cyclic activity (SAFRIEL, 1969; HUGHES, 1971; WARBURTON, 1973; RUWA & BRAKEL, 1981; GARRITY, 1984), selective use of microhabitats (GARRITY, 1984), evaporative cooling (VERMEIJ, 1971, 1973), formation of multilayered aggregations (GARRITY & LEVINGS, 1984), and establishment of shore-level size gradients (FRANK, 1965; VERMEIJ, 1972). Gastropods may also aggregate in response to distribution of food resources (UNDERWOOD, 1976), and shore-level size gradients sometimes reflect selective predation (VERMEIJ, 1972; MCCORMACK, 1982). In tropical environments, competition (UNDERWOOD, 1976, 1978; BLACK, 1979; ORTEGA, 1985) and predation (BERTNESS *et al.*, 1981; BERTNESS & CUNNINGHAM, 1981; GARRITY & LEVINGS,

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1981, 1983; MENGE & LUBCHENCO, 1981; CHILTON & BULL, 1984) may strongly affect abundance patterns of gastropods. While these and other results (RUWA & JACCARINI, 1986) emphasize the varied responses possible for mobile intertidal organisms, surprisingly few studies have focused on physiological or behavioral responses of gastropods following transplant above or below their natural vertical range. The present study examines an aspect of the proximate mechanism that results in the maintenance of shore-level gradients in gastropods.

The herbivorous gastropod genus *Nerita* is common throughout the tropics and subtropics, and zonation of most species reflects the tidal gradient (VANNINI & CHELAZZI, 1978; GARRITY & LEVINGS, 1981; RUWA & JACCARINI, 1986). *Nerita versicolor* Gmelin, 1791, whose geographic range includes Bermuda and south Florida to Brazil (EMERSON & JACOBSON, 1976; ABBOTT, 1986), is usually characteristic of high-shore locations during low tide (HUGHES, 1971; VERMEIJ, 1973). In Caribbean waters, the littorinid gastropod *Nodilittorina* (*Tectininus*) *antoni* (Philippi, 1846) (BANDEL & KADOLSKY, 1982) joins *Nerita versicolor* on rocky shores. Although their distribution at low tide is overlapping for a portion of their vertical range, *Nerita versicolor* extends into the lower mid-intertidal zone, while *Nodilittorina antoni* usually predominates in the high intertidal zone in the Bahamas. Here, we examine snail abundance and distribution in response to the tidal gradient and microhabitat characteristics. We seek to determine whether zonation and behavioral patterns of these prosobranch gastropods are related to physiological limitation, habitat characteristics, or biological interactions.

MATERIALS AND METHODS

Study Sites

In order to document snail distribution in relation to substratum heterogeneity and slope of the shore, *Nerita versicolor* and *Nodilittorina antoni* were examined at five sites in the Bahamas, all with predominantly west-facing exposure. The substratum at all sites was lithified carbonate beach sand (eolianite beachrock). The primary study area (site 1) at San Salvador Island (24°03.0′N, 74°33.0′W) had a slope of 60° and tidepools occurred throughout the intertidal zone. The rock surface was heavily pitted by small, deep depressions in high intertidal areas (60% of the surface) and became smoother in the seaward direction. Only 20% of the rock surface was pitted in low intertidal regions. An area with similar slope and microhabitat structure was studied at Man O War Cay (26°36.3′N, 77°01.0′W, site 2). Three additional sites were studied at San Salvador Island. Site 3 had a slope of 45°, decreased pitting downshore (70% and 10% of the surface in high and low intertidal areas respectively), and no tidepools. Site 4 (slope 20°) had shallow pits (60% of surface) in the mid-intertidal, while high and low intertidal areas had a relatively flat, open-faced topography. Tidepools were rare (<5% of surface) at this site. Site 5 (slope 20°) contained deep pits (50% of surface) in high intertidal areas; low intertidal topography was predominantly tidepools alternating with ridges. Measurements were taken during January 1986 and 1987 at San Salvador Island sites and during March 1986 at Man O War Cay.

The most abundant intertidal gastropod species at all sites were the herbivorous prosobranchs *Nerita versicolor* and *Nodilittorina antoni*. Other components of the gastropod assemblage, including *Nerita peloronta* Linnaeus, *Nerita tessellata* Gmelin, and *Nodilittorina tuberculata* Menke, occurred in low abundance. The rocky substratum showed a patchy distribution (up to 30% cover) of encrusting cyanobacteria; other attached organisms (*e.g.*, barnacles and macroalgae) were rare.

Methods

Based on preliminary observations during low tide of the distribution patterns of *Nerita versicolor* and *Nodilittorina antoni* at site 1, three intertidal zones were defined for study: (1) a high zone, at approximately +1.4 m above mean low water (MLW), where *Nodilittorina antoni* predominated, (2) the high-mid zone, at approximately +0.9 m above MLW, where the two snails showed greatest overlap, and (3) the low-mid zone, at +0.5 m above MLW, where *Nerita versicolor* predominated. Height measurements were made with level and stadia. The zones of sites 4 and 5 were compressed vertically owing to the more gentle slope of the shore. Abundance of *Nerita versicolor* and *Nodilittorina antoni* were measured during low tide by sampling 0.09-m^2 quadrats (n = 8 to 16) located at 0.5-m intervals along a horizontal transect situated at the approximate center of each of the three zones at the five sites. Within the zones, microhabitat use was quantified by recording the characteristics of the rock on which the snails occurred, *e.g.*, pitted, tidepool, or flat.

Size-frequency distributions by zone were determined at site 1, San Salvador Island, by collecting all individuals within several 0.09-m^2 quadrats used for density estimates. We measured shell length (aperture to apex) to the nearest 0.1 mm using Vernier calipers.

We examined epilithic crusts in each zone at sites 1 and 4 in order to qualitatively relate microalgal abundance to snail distribution patterns. The crusts were scraped from 0.16-cm^2 quadrats with a razor blade and examined with a compound microscope. In addition, gut contents of both snail species were assessed. Specimens preserved in 10% formalin solution were returned to the laboratory and dissected; gut contents were examined with a compound microscope.

We determined whether the observed vertical distribution patterns were related to physiological limitation, *i.e.*, desiccation or intolerance of long-term submergence. Plastic containers (20 × 20 × 6 cm), from which the bottoms were removed, were fastened to the rocky substratum with masonry nails at 0.0 m (below the range of

Table 1

Relative proportions of *Nodilittorina antoni* and *Nerita versicolor* in different microhabitats during daytime low tide at San Salvador Island, Bahamas. Data were pooled for sites 1, 3, 4, and 5 across tidal zones.

Species	*n*	Microhabitat type		
		Flat	crevice/pit	Tidepool
Nodilittorina	1656	0.17	0.81	0.01
Nerita	563	0.34	0.60	0.06

either species) and at +1.7 and +2.0 m (above the range of either species). Individuals of both species were enclosed in the containers, which were covered by screen (mesh size = 4 mm). The shading from the screen reduced the midday substratum temperature approximately 1.5°C relative to the adjacent rock surface. Snail survivorship (n = 20, each treatment) was determined after six days. In addition, snails were held submerged in running seawater (in the laboratory) or emerged in open containers receiving midday sun in order to determine tolerance of continual submergence (n = 50, each species) and emergence (n = 50, each species) respectively. Loss of fresh weight by marked individuals (n = 10, each species) held in the open containers was determined daily for six days.

Transplant experiments were designed to assess snail movement in relation to tidal height and the presence or absence of the other snail species. Snails were collected throughout their vertical range at sites 1 and 2. The shells were numbered in the laboratory with indelible ink (*Nerita*) or with a numbered 2 × 2-mm tag glued to the shell (*Nodilittorina*); clear Superglue™ sealed the markings. Although marked *Nerita* had the same size distribution as the natural population, the mean size of marked *Nodilittorina antoni* was greater than the natural population owing to difficulties of marking very small snails. The snails were returned to the site at the next low tide, placed on wetted rock surfaces in the high and low-mid zones at naturally occurring densities. For *Nodilittorina antoni,* snails returned in the high zone were within their vertical range (control treatment), but above the range of *Nerita versicolor,* while snails placed in the low-mid zone were below their vertical range, but within the range of *Nerita versicolor.* The opposite transplant conditions were true for *Nerita versicolor.* The effect of interspecific interactions on movement patterns was determined by comparing response of snails placed into areas where the other species occurred in natural abundances with a removal treatment. For this latter treatment, *Nerita versicolor* and *Nodilittorina antoni* were removed from experimental areas (ca. 6 m²) within the low-mid and high zones, respectively, where the other species had been placed. This method of snail removal was effective for the duration of the experiment; the few (<5 per m²) immigrating snails were removed daily from each area. Location of marked snails was determined after two and six tidal cycles (site 1) or one tidal cycle (site 2).

One-way analysis of variance (ANOVA) or t-tests were used to establish significant differences for means of density and weight loss measurements; Mann-Whitney U-tests were used for comparisons of size-frequency distributions (Sokal & Rohlf, 1981). The Student-Newman-Keuls (SNK) procedure was applied to significant ANOVA tests. The relationships between time and weight loss and between microhabitat features and snail density were determined using linear regression. Chi-square analyses established the significance of movement patterns following various transplant conditions.

RESULTS

Zonation Patterns

Microhabitat selection: Observations made during falling and incoming tides revealed that both species were inactive once the water dropped below their vertical position on the rock, and usually did not move again until splashed by rising water. During daytime low tides, the highest proportion of both species, particularly *Nodilittorina antoni* (hereafter as *Nodilittorina*), were lodged in crevices or pits (Table 1). Results from regression analysis revealed a significant positive relationship (r^2 = 0.79, F = 14.9, P < 0.02) between snail density and occurrence of pits in the high zone for *Nodilittorina.* While density of *Nerita versicolor* (hereafter as *Nerita*) was negatively related (r^2 = 0.90, F = 34.1, P < 0.01) to the occurrence of pits in the high zone, snail number and substratum pitting were positively correlated (r^2 = 0.79, F = 11.0, P < 0.05) in the high-mid zone. One-third of the sampled *Nerita* were also found on relatively flat rock; this surface occurred predominantly in the low-mid zone. Few snails occurred in tidepools despite the relatively high abundance of this microhabitat throughout the range of both of these snails.

Slope of the shore had limited effect on snail distribution patterns at low tide. *Nodilittorina* density was not related to slope of the shore except in the high zone (r^2 = 0.96, F = 87.6, P < 0.001). There was no apparent relationship (P > 0.05) between *Nerita* density and shore inclination in any of the zones.

Size gradients and abundances: Mean size of *Nodilittorina* and *Nerita* increased significantly in the downshore direction at site 1 (Figure 1). For example, during January 1986 and 1987, mean size of *Nerita* was greater (P < 0.01, Mann-Whitney U-test) in the low-mid than high-mid zones. Mean size of *Nodilittorina* was greater (P < 0.05, Mann-Whitney U-test) during 1987 than 1986 at both tidal levels, concomitant with a significant decrease in size of *Nerita* during the same period in the high-mid zone, the area of overlap.

Distinctive abundance patterns with tidal height were evident for both species at sites 1, 2 and 3 (Table 2). *Nodilittorina* rarely occurred in the low-mid zone while

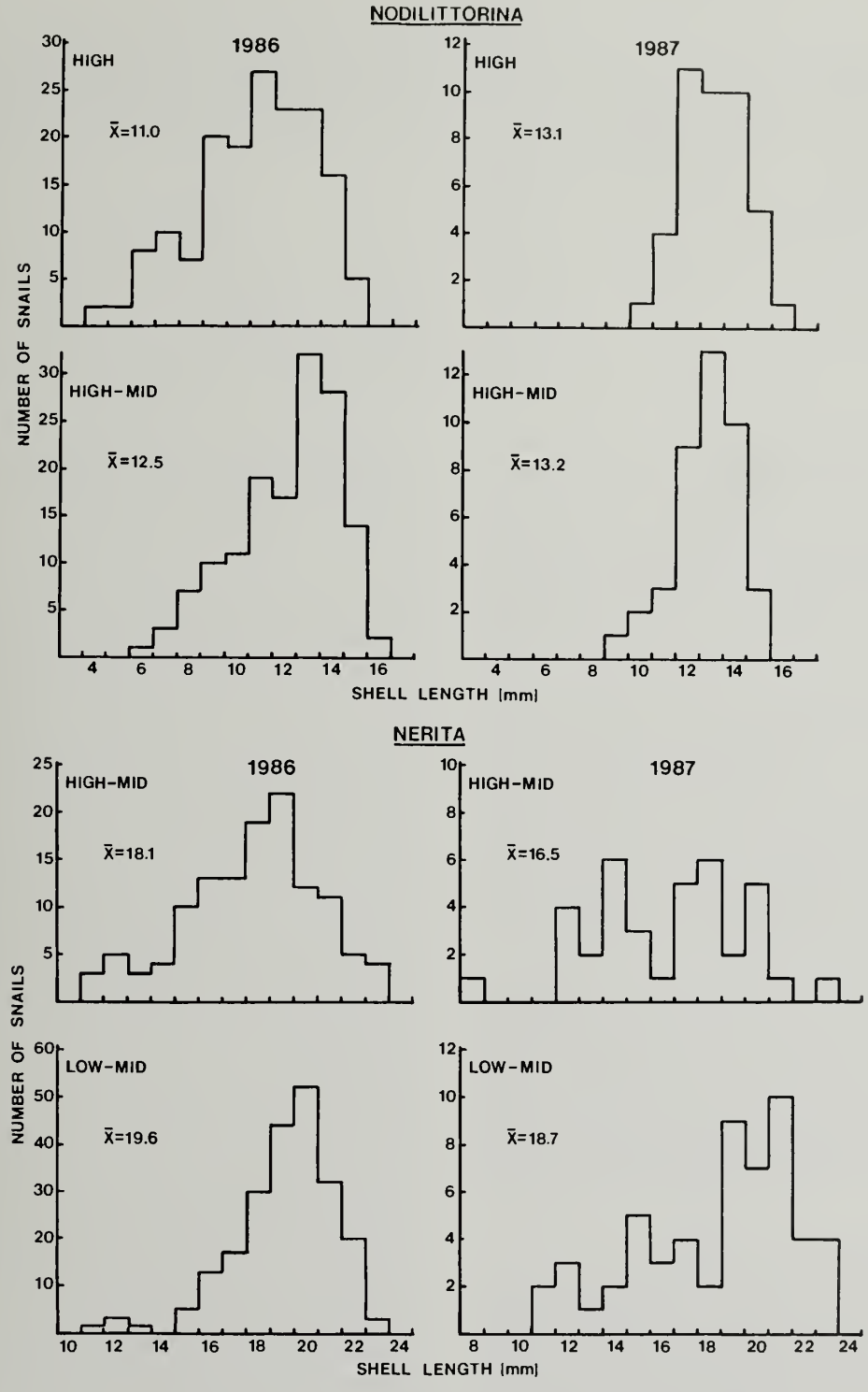

Figure 1

Size-frequency distributions of *Nodilittorina antoni* and *Nerita versicolor* with tidal height during January 1986 and 1987 at site 1. Mean ($\bar{x}$) size (mm) is indicated for each zone.

Table 2

Densities (mean number ± SE per m^2) of *Nodilittorina antoni* and *Nerita versicolor* by zone at five sites in the Bahamas. Sampling dates: site 1, January 1986 and 1987; site 2, March 1986; sites 3–5, January 1987.

Zone	Species	Site 1		Site 2	Site 3	Site 4	Site 5
		1986	1987				
High	*Nodilittorina*	259 ± 71	240 ± 49	312 ± 109	201 ± 50	18 ± 4	32 ± 6
	Nerita	0	4 ± 2	0	0	44 ± 10	11 ± 4
High-mid	*Nodilittorina*	110 ± 58	95 ± 28	46 ± 19	116 ± 38	272 ± 56	78 ± 18
	Nerita	36 ± 11	29 ± 7	30 ± 9	11 ± 6	56 ± 11	57 ± 9
Low-mid	*Nodilittorina*	0	6 ± 4	0	0	16 ± 6	3 ± 1
	Nerita	56 ± 16	31 ± 12	124 ± 41	33 ± 14	6 ± 4	72 ± 16

Nerita was usually absent from the high zone at these sites. Except for the 1987 sample of *Nerita* at site 1, both species had lower densities ($P < 0.05$, t-tests) in the high-mid zone, the area where they showed greatest overlap. In fact, densities of the two species were negatively correlated at the three sites (Pearson product-moment correlation coefficients: site 1, $r = -0.28$, $P < 0.05$; site 2, $r = -0.51$, $P < 0.01$; site 3, $r = -0.47$, $P < 0.01$). Although densities of *Nodilittorina* at site 1 were similar during 1986 and 1987, *Nerita* was less abundant during 1987 than 1986.

Snail distribution patterns at sites 4 and 5 contrasted with those of the other sites (Table 2). *Nodilittorina* was more abundant ($P < 0.05$, SNK) within the high-mid zone, particularly of site 4, rather than the high zone. In fact, there were significantly fewer *Nodilittorina* in the high zone at sites 4 and 5 than at the other three sites. *Nerita* had relatively high abundance in the high zone, and low density in the low-mid zone at site 4 ($P < 0.05$, SNK), a reversal of its distribution pattern at all other sites.

Food availability: Crusts scraped off the rocks from the three zones at sites 1 and 4 indicated that cyanobacteria, particularly *Oscillatoria* sp., *Calothrix* sp., and *Anacystis* sp., predominated throughout the vertical range of the two gastropods. Qualitative (visual) estimates indicated that biomass of these encrusting species was inversely related to tidal height. Gut contents of *Nodilittorina* and *Nerita* were similar, and reflected the relative abundances of the cyanobacteria.

Response to Transplant Conditions

Continual submersion and emersion: Results of the continual submergence and emergence tests indicated that *Nodilittorina* and *Nerita* had a vertical distribution at low tide that was well within their physiological range. For example, both species survived one week of continual submergence. All snails survived within enclosures placed above their vertical ranges; however, *Nodilittorina* had greater percentage weight loss ($P < 0.001$, t-test) than *Nerita* after a 24-h period of continual emergence. Following this initial water loss, both species had the same rate of weight loss for the next five days (slopes of both linear regressions, $b = 0.03$, for days two through six; Figure 2). Enclosures placed below the range of either species were removed by heavy wave action during a storm.

Movement patterns: Results from the control treatments for the transplant experiments of *Nerita* and *Nodilittorina* indicated little effect from handling the snails (Table 3). At site 2, 100% of both species that were marked and replaced in their respective zones were recovered. The mean recoveries of snails from the control treatment during the two transplant experiments at site 1 were 89% and 88% for *Nerita* and *Nodilittorina* respectively.

Snail movement patterns following transplant were independent of occurrence ($P > 0.10$, Chi-square tests) of the other species (Table 3). For example, at site 2, all recovered *Nerita* and *Nodilittorina* that had been transplanted to the high-mid and low-mid zones respectively, showed similar movement patterns in the presence and absence of the other species. Thus, for subsequent statistical analyses and discussion, we pooled those data, and focused on assessing snail response to placement at various tidal locations.

Recovery location following transplant was, in part, dependent on the length of time between initiation of the experiment and subsequent sampling (Table 3). Snails placed in the zone where they had highest natural abundance were usually recovered in the same zone, regardless of the time interval following placement. The exceptions, three *Nerita* that moved into a high intertidal pool following placement in the low-mid zone, remained there for the duration of this experiment. At site 1, 28% (during 1986) and 40% (during 1987) of *Nerita* transplanted into the high zone (above its usual range) remained there after two tidal cycles. However, for the 1987 transplant experiment, 26% of those snails recovered in the high zone were located in tidepools. Similarly, 21% (during 1986) and 23% (during 1987) of *Nodilittorina* transplanted into the low-mid zone (below its usual range) remained there after two tidal cycles. At site 2, all recovered *Nerita* transplants had returned downshore to their natural zone after one tidal

cycle, while less than one-half of the transplanted *Nodilittorina* had moved upshore to their zone within the same period. After six tidal cycles at site 1, all but one recovered *Nodilittorina* transplant had returned upshore; the only *Nerita* remaining in the high zone after this period were located in tidepools.

DISCUSSION

This study documented site-specific zonation patterns of *Nerita versicolor* and *Nodilittorina antoni* in the Bahamas. Although *Nerita* is characteristic of high-shore locations on both horizontal and vertical surfaces (HUGHES, 1971; VERMEIJ, 1973), in the present study this species extended above the high-mid zone only at a site with reduced microtopography, where *Nodilittorina* was less abundant. *Nerita* was extremely rare in high zones of sites etched with small pits. In contrast, *Nodilittorina* predominated in high-shore regions but was rarely observed below the high-mid zone. In fact, interspecific densities were negatively correlated at three sites. This zonation pattern was re-established following transplant of the snails outside of their vertical range. The zonation and behavioral patterns of these intertidal gastropods thus suggest an active response to microhabitat characteristics or species interactions.

Based on continual emersion and submersion tests, the vertical distribution of both snails at low tide was well within their physiological limits. The nodulose shell sculpture of many high intertidal littorinids, including *Nodilittorina,* may aid in heat loss from the shell surface (VERMEIJ, 1971, 1973). Neritid gastropods are also well-adapted to high temperature and desiccation stresses owing to their morphology and behavior. Many species have a large extravisceral reservoir, capable of holding water used in evaporative cooling. Increased shell globosity, as characteristic of *Nerita versicolor,* both enhances water-holding capacity and decreases the area and perimeter of the base in contact with the substratum. Most nerites can enter into a dormant state fully retracted into the shell behind a thick operculum (VERMEIJ, 1973). Thus, absence of *Nerita versicolor* from the high zone of most sites was probably not due to physiological limitation.

Nerita and *Nodilittorina* were inactive once water retreated during daytime low tides, and occurred predominantly in pits or crevices during this period. Use of crevices as refuges by gastropods on tropical rocky shores reduces the risk of mortality due to desiccation or heat stress (LEVINGS & GARRITY, 1983; GARRITY, 1984). RAFFAELLI & HUGHES (1978) reported a positive relationship between abundance of littorinid gastropods and the availability of crevices, and suggested that snails without this refuge were often dislodged by wave action. In the present study, either of these factors might, in part, explain the lower abundances of *Nodilittorina* in regions such as high shore at site 4 and low intertidal areas, where such microtopography was lacking. Because the two species varied greatly in size, the small, deep pits characteristic of the high intertidal

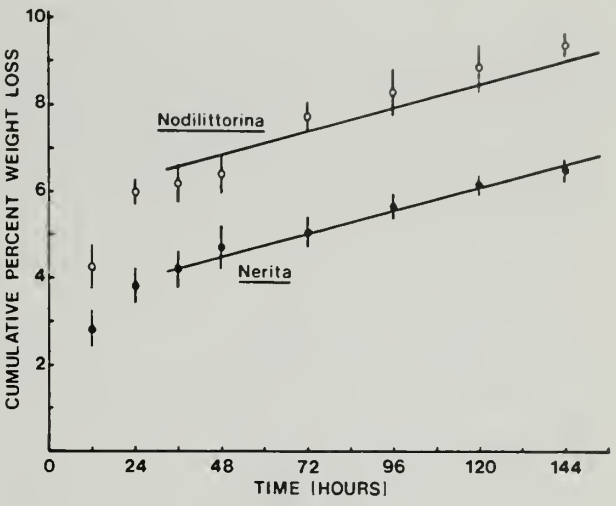

Figure 2

Cumulative percent weight loss with time (mean values ± SE) of *Nodilittorina antoni* and *Nerita versicolor* during continual exposure to air. After 24 h, linear regression analyses generated the following equations: for *Nodilittorina* $y = 0.03x + 5.29$; for *Nerita* $y = 0.03x + 3.32$.

regions in four of the five sites may not accommodate most *Nerita*. Perhaps *Nerita* is dislodged from such highly irregular surfaces by wave action.

FLETCHER & UNDERWOOD (1987) documented a complex relationship among substratum heterogeneity, competitive interactions between two limpet species, and grazing urchins. On smooth substrata, "bulldozing" by the larger congener and crushing by grazing urchins reduced densities of the smaller limpet, *Patelloida mufria*; this interaction did not occur on pitted surfaces. In the present study, the site-specific zonation patterns of *Nerita* and *Nodilittorina,* the significant negative correlations between interspecific densities at pitted sites, the concomitant decrease in size of *Nerita* with increase in size of *Nodilittorina* during 1987 at site 1, and the regular spacing pattern ($P < 0.05$, nearest neighbor analysis, CLARK & EVANS, 1954) documented for each species in the region of overlap (Peckol, unpublished data) suggest a species interaction mediated by microhabitat characteristics.

Because snails returned to their respective zones following transplant outside their vertical range both in the presence and absence of the other species, it is unlikely that distribution patterns are due to interference competition. Intra- and interspecific competition for food have been shown to affect density and growth of intertidal gastropods (HAVEN, 1973; UNDERWOOD, 1976; LEVINTON, 1985). Gut analyses indicated that the two snails in this study have a similar diet, primarily cyanobacteria. Although UNDERWOOD (1978) suggested that the radular design of neritid gastropods permitted rapid, effective foraging of the surface microalgae, possibly *Nerita versicolor* does not forage

Table 3

Recovery of *Nodilittorina antoni* and *Nerita versicolor* after one to six complete tidal cycles following transplant of snails within and outside their vertical range in the presence (+) and absence (−) of the other species at sites 1 (San Salvador Island) and 2 (Man O War Cay). For *Nodilittorina,* within = high and high-mid zones, outside = low-mid zone; for *Nerita,* within = high-mid and low-mid zones, outside = high zone. TP = snail found in a tidepool within a particular zone.

Transplant condition		*n*	Percent recovered	Number recovered	
				Within zone	Outside zone
Site 1:					
January 1986, 2 tidal cycles					
Nodilittorina	Within zone	37	84	31	0
	Outside zone (+)	38	84	24	8
Nerita	Within zone	40	80	32	0
	Outside zone (+)	40	84	22	11
January 1987, 2 tidal cycles					
Nodilittorina	Within zone	33	92	30	0
	Outside zone (+)	30	97	21	8
	Outside zone (−)	32	100	26	6
Nerita	Within zone	31	94	26	3 (TP)
	Outside zone (+)	36	92	16	11 + 6 (TP)
	Outside zone (−)	32	94	18 + 2(TP)	9 + 1(TP)
January 1987, 6 tidal cycles					
Nodilittorina	Within zone	33	78	26	0
	Outside zone (+)	30	80	24	0
	Outside zone (−)	32	100	31	1
Nerita	Within zone	31	84	23	3 (TP)
	Outside zone (+)	36	78	26	2 (TP)
	Outside zone (−)	32	72	23	0
Site 2:					
March 1986, 1 tidal cycle					
Nodilittorina	Within zone	50	100	50	0
	Outside zone (+)	50	88	19	25
	Outside zone (−)	50	90	21	24
Nerita	Within zone	29	100	29	0
	Outside zone (+)	50	94	47	0
	Outside zone (−)	50	82	41	0

effectively over deeply pitted surfaces characteristic of the high zones of several sites. Larger snails often move greater distances than smaller individuals during foraging activities (Ruwa & Brakel, 1981; Levings & Garrity, 1983; Garrity & Levings, 1984). Thus larger *Nerita versicolor* may forage greater distances, enabling the species to benefit from the more abundant food resource of the lower intertidal region.

In addition to density differences along the tidal gradient, both species showed an inverse relationship between tidal height and shell size. Selective predation in lower intertidal areas might result in this size gradient (Vermeij, 1972; Chilton & Bull, 1984). The impact of predatory fish, crabs, and snails on foraging patterns and survival of tropical gastropods has been investigated (Safriel, 1969; Hughes, 1971; Bertness *et al.,* 1981; Garrity & Levings, 1981, 1983). Although size selection by predatory crabs has been documented (Elner & Hughes, 1978; Bertness & Cunningham, 1981; Chilton & Bull, 1986), Bertness *et al.* (1981) found that fish crushed the largest (20.5 mm) neritid gastropod offered. Additional work is necessary in order to determine if selective predation contributes to the intra- and interspecific shore-level size gradients observed in this study.

The shore-level gradients of size and density maintained by intertidal gastropod populations in response to food or microhabitat availability, or to selective predation, are clearly finely tuned relative to zonation patterns of sessile organisms. The variations in distribution patterns with site, documented in this study, and time (Ruwa & Brakel, 1981; Levings & Garrity, 1983; Ruwa & Jaccarini, 1986) emphasize the dynamic nature of processes operating in rocky intertidal, particularly tropical, habitats.

ACKNOWLEDGMENTS

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Evaporative Water Loss from Minute Terrestrial Snails (Pulmonata: Pupillidae)

by

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Abstract. Rates of evaporative water loss (weight loss) were measured in six species of Pupillidae ranging in mass from 0.7 to 12 mg. These minute terrestrial snails are of interest because of their high surface-volume ratio and consequent potential susceptibility to water loss. Water loss of dormant individuals was 0.30 to 0.35% of initial body water per day during one month of dormancy at 5% RH, 22°C. Compared on the basis of surface area, water loss of these species during dormancy appears to be the lowest yet observed among land snails, including species having three or four orders of magnitude greater mass and much thicker shells. Shell permeability to water may be two orders of magnitude lower than that of helicids. Although pupillids are capable of surviving several months of dormancy in dry air, active (crawling) individuals lost water up to 17,900 times faster than dormant snails and remained active for only 5–15 min at 60% RH, 22°C. Minute land snails may be particularly constrained to arouse from dormancy only when free water is available to offset evaporative loss.

INTRODUCTION

Control of evaporative water loss (EWL) by behavioral or physiological means is prerequisite to life on land. Among the few phyla that have taken up non-burrowing terrestrial habits, the water relations of shelled land snails are unique. The integument of active snails presents no significant resistance to evaporation, so that activity depends on the availability of moisture. In dehydrating conditions snails retract into the shell and enter a state of dormancy, during which the shell and mantle collar, together with reduced lung ventilation, effectively waterproof the animal and permit prolonged survival (MACHIN, 1975; RIDDLE, 1983; PRIOR, 1985; BARNHART, 1986).

Control of EWL is presumably especially critical in species of small size (RIDDLE, 1983). As size decreases, the ratio of surface area to volume increases. Moreover, the thickness of the shell may decrease and consequently permeability to water may increase. Water loss has previously been investigated mainly in species weighing several grams (CAMERON, 1970; MACHIN, 1975; RIDDLE, 1975; HEATWOLE & HEATWOLE, 1978). Very little is known of the capabilities of the numerous minute species of land pulmonates (WARBURG, 1965). Therefore, it is of interest to examine water loss in species of the family Pupillidae, which are relatively small among land pulmonates (adult mass about 0.5 to 15 mg). Pupillids are common in grassland and forest habitats of midwestern North America (LEONARD, 1959).

MATERIALS AND METHODS

Water loss was measured in the following species of Pupillidae during dormancy: *Gastrocopta armifera, G. contracta, G. procera, G. holzingeri, Pupoides albilabris,* and *Vallonia costata.* The effects of relative humidity (RH) and temperature on EWL were examined in detail in dormant *G. armifera,* and EWL of active individuals was measured in *G. armifera* and *G. procera.*

Snails were collected on the campus of the University of Kansas, Lawrence, Kansas. After collection the snails were held in terraria on damp paper toweling for 1–2 days to permit hydration. Individuals that failed to become active were discarded. Each snail was then placed in a vial capped with nylon mesh to allow free air circulation. The vials were placed in larger containers containing desiccant (Drierite®) or saturated salt solutions to maintain 0% (desiccant), 5% (NaOH), 33% ($MgCl_2$), or 75% (NaCl) RH (WINSTON & BATES, 1960). The snails ceased activity within minutes of removal from moisture. After 1 week and subsequently at intervals each individual was removed from its vial and weighed to the nearest microgram using

Table 1

Mass of dormant pupillid snails after 1 week of dormancy. Data are mean ± SD. n = 20 for each species.

	Total mass (mg)	Water mass (mg)	Water mass (% total)	Shell mass (% total)
Gastrocopta armifera	12.237	5.43	44.39	47.77
	±1.269	±0.630	±2.41	±2.84
G. contracta	2.763	1.18	43.01	49.40
	±0.337	±0.148	±4.44	±5.23
G. procera	1.942	0.863	44.79	47.30
	±0.400	±0.173	±5.27	±6.20
G. holzingeri	0.724	0.283	39.11	53.99
	±0.060	±0.027	±2.85	±3.35
Pupoides albilabris	9.994	4.66	46.98	44.73
	±1.734	±0.735	±5.36	±6.31
Vallonia costata	1.316	0.652	49.70	41.53
	±0.168	±0.087	±4.61	±5.43

a Cahn gram electrobalance. The balance was tared regularly during use to ensure that drift did not impair accuracy.

To measure EWL during activity, active snails were placed in a shallow plastic pan suspended from the weighing arm of the electrobalance. Relative humidity in the weighing chamber was measured using a Honeywell humidity sensor and remained at about 60% (57–65%). Mass was recorded each minute until the snail ceased crawling and retracted into the shell.

Weight loss was presumed to reflect water loss exclusively. However, some mass must also be lost as carbon in CO_2 production; if dry mass is lost in proportion to water during dormancy (SCHMIDT-NIELSEN *et al.*, 1971; HORNE, 1973), water loss may be 10–15% lower than total weight loss. After weight loss measurements the snails were dried to constant mass at 70°C. Total body water was determined as the difference between wet and dry mass. Tissue mass was estimated from total body water by assuming tissue to be 85% water (MACHIN, 1975). Shell mass was estimated by subtracting tissue mass from total mass.

Water vapor pressure difference (VPD) between tissues and ambient air was calculated based on temperature and RH and by assuming saturation at the tissues. Vapor

Table 2

Weight loss of dormant pupillids at 5% and 75% relative humidity (22°C) during two consecutive months of dormancy. Values are mean ± SD (n). Mass-specific loss rates are percent initial body water per day.

	5% RH				75% RH			
	First month		Second month		First month		Second month	
	μg day^{-1}	% day^{-1}	μg day^{-1}	% day^{-1}	μg day^{-1}	% day^{-1}	μg day^{-1}	% day^{-1}
Gastrocopta armifera	49.2	0.915	19.0	0.349	32.0	0.583	16.5	0.305
	±14.6	±0.262	±6.93	±0.117	±8.83	±0.134	±6.57	±0.127
	(10)	(10)	(7)	(7)	(10)	(10)	(10)	(10)
G. contracta	8.84	0.701	4.33	0.346	4.21	0.367	2.31	0.201
	±2.28	±0.124	±1.06	±0.076	±1.40	±0.093	±0.88	±0.063
	(8)	(8)	(8)	(8)	(9)	(9)	(9)	(9)
G. procera	6.57	0.779	2.50	0.299	3.89	0.452	2.01	0.225
	±2.96	±0.269	±0.69	±0.057	±0.98	±0.130	±0.81	±0.066
	(10)	(10)	(10)	(10)	(10)	(10)	(10)	(10)
G. holzingeri	1.27	0.452	0.99	0.349				
	±0.16	±0.054	±0.14	±0.039	—	—	—	—
	(20)	(20)	(20)	(20)				
Pupoides albilabris	34.1	0.734	18.1	0.376				
	±6.72	±0.206	±3.22	±0.059	—	—	—	—
	(9)	(9)	(7)	(7)				
Vallonia costata	5.28	0.784	2.32	0.353	3.82	0.573	3.60	0.549
	±1.15	±0.101	±0.49	±0.092	±1.59	±0.209	±1.73	±0.254
	(10)	(10)	(10)	(10)	(9)	(9)	(9)	(9)

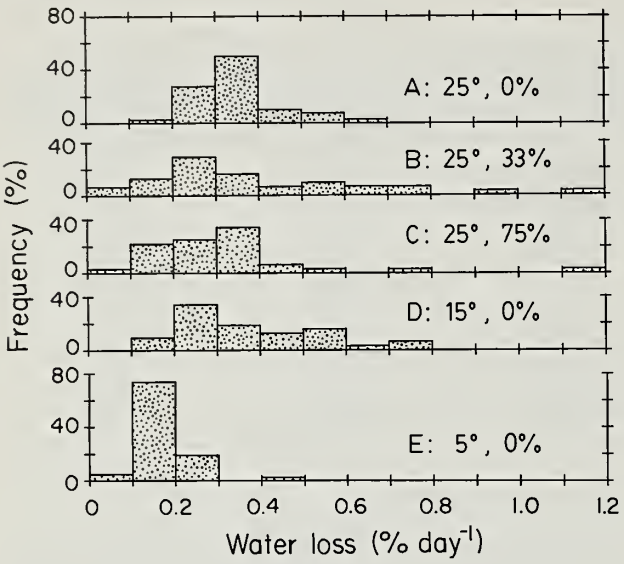

Figure 1

Frequency distributions of weight loss from dormant *Gastrocopta armifera* in the indicated conditions of temperature and humidity. The distributions differed significantly ($P < 0.05$) in all but two (A vs. B, B vs. D) of the possible 10 pairwise comparisons. Means are shown in Table 3.

pressure difference is directly related to the difference in chemical potential of water and therefore to the force driving evaporation and diffusion of water vapor (Edney, 1977).

The Kruskal-Wallis test was used to test for significant differences among species and treatment groups, followed by nonparametric multiple comparisons using rank sums according to Zar (1984:199). Critical P was 0.05.

RESULTS

Interspecific Comparison

Mean individual mass ranged from 0.7 to 12.2 mg among the six species. Ranges of initial water content and shell mass among the species were 39–50% and 41–54% of total mass respectively (Table 1). Weight loss was significantly lower during the second month than during the first month of dormancy in all species except *Vallonia costata* at 75% RH (Table 2). Mass-specific EWL rates during the second month of dormancy did not differ significantly among the species (Table 2) and averaged 0.35% day^{-1} at 5% RH.

Effects of Humidity and Temperature

Evaporative water loss was significantly higher at 5% than at 75% RH in all species except *Vallonia costata* (Table 2). However, the increase was always less than two fold, whereas VPD was nearly four fold greater at 5% RH (16.6 torr) than at 75% RH (4.4 torr). In a more detailed test of humidity and temperature effects, mean EWL of dormant *Gastrocopta armifera* again was not proportional to vapor pressure deficit (Table 3). The distributions of individual losses were skewed, with some individuals showing relatively large losses (Figure 1).

Table 3

Effects of temperature, relative humidity, and vapor pressure deficit on water loss of dormant *Gastrocopta armifera*. Mass-specific loss rates are percent initial body water per day; mean ± SD (n).

Temp. (°C)	Humidity (%)	VPD (torr)	Water loss (% day^{-1})
25	0	23.8	0.352 ± 0.088 (40)
25	33	15.9	0.445 ± 0.271 (40)
15	0	12.8	0.371 ± 0.159 (39)
5	0	6.5	0.225 ± 0.076 (38)
25	75	6.0	0.331 ± 0.194 (39)

Mortality

Nineteen of 40 *Gastrocopta armifera* died during 2.5 months of dormancy at 25°C, 0% RH (specimens kept in other conditions were observed for only 2 months and nearly all survived). The mean (±SD) weight loss before death was 30.5% ± 7.6 of initial water mass and did not differ significantly from the mean loss of the 21 survivors (32.8% ± 5.9). Eight of 40 individuals lost 40–50% of initial water mass before death. Thus, death cannot be attributed unambiguously to a critical level of dehydration.

Water Loss During Activity

Active (crawling) snails lost water at vastly higher rates than dormant individuals (Table 4). The factorial increase over minimum dormant EWL (Table 2, month 2, 75% RH) was 5448 and 17,910 for *Gastrocopta armifera* and *G. procera* respectively. Snails continued crawling for only 5–15 min before retracting into the shell. Within 5 min of retracting, EWL of *G. armifera* declined by 92% (Table 4).

DISCUSSION

Size and Water Loss

A priori, higher mass-specific and area-specific EWL were expected in pupillids than in larger pulmonates, based on two assumptions: (1) EWL is limited by the water conductance of surface barriers (shell and mantle collar) and (2) shell form is roughly isometric, so that smaller snails have higher surface-volume ratio and thinner shells. Let A = shell surface area, L = thickness, V = volume, G = water conductance, and M = body mass. Theoretically, $G \propto A/L$. For a shell of constant proportions, $A \propto V^{2/3}$ and $L \propto V^{1/3}$, thus $G \propto V^{1/3}$. Assuming $M \propto V$, predicted mass-specific EWL $\propto M^{-2/3}$ and area-specific EWL $\propto M^{-1/3}$. An individual weighing 1 mg is thus expected to lose

Table 4

Water loss from active (crawling) pupillids (*Gastrocopta*) at 60% RH, 22°C (mean ± SD).

	G. armifera (n = 8)	*G. procera* (n = 5)
Initial total mass	10.25 ± 1.13 mg	1.85 ± 0.15 mg
Initial water mass	4.98 ± 0.43 mg	0.904 ± 0.075 mg
Water loss while crawling	89.9 ± 9.56 mg day^{-1}	36.0 ± 3.43 mg day^{-1}
	1806 ± 138% day^{-1}	3977 ± 112% day^{-1}
Water loss 5 min after retracting	7.2 ± 0.50 mg day^{-1}	—
	145 ± 5.6% day^{-1}	—
Water lost before retracting	12.3 ± 5.1%	—

water 464 times faster per unit mass and 46.4 times faster per unit area than one weighing 10 g.

In contrast to these predictions, the available data show that mass-specific EWL of dormant pulmonates differs only about 10 fold, rather than 464 fold, over a 10,000-fold range of mass (Figure 2). Surface areas were not measured, but approximate comparisons of area-specific EWL can be made by extrapolating the mass-specific EWL of the small species to larger mass, assuming surface area proportional to $mass^{2/3}$. This extrapolation for the smallest pupillids indicate that the area-specific EWL is lower than that of the larger species, including the highly xerophilous *Sphincterochila* (Figure 2).

Pupillids evidently match the low area-specific water conductance of much larger species in spite of much thinner shells. The shell mass of pupillids as a proportion of whole mass (41–54%, Table 1) is similar to that of larger xeric-adapted species such as *Trochoidea* (38%), and *Sphincterochila* (48–56%) (Yom-Tov, 1971; Schmidt-Nielsen *et al.*, 1971), indicating that the shell is not disproportionately thicker in pupillids. The shell thickness of *Sphincterochila* (0.84 mm; Machin, 1967) matches the entire shell diameter of *Gastrocopta holzingeri* (about 0.88 mm).

Permeability of the shell material to water may be far lower in pupillids than in the larger helicid pulmonates. The water permeability coefficient of helicid shells is approximately 0.003 $mg \cdot mm \cdot cm^{-2} \cdot day^{-1} \cdot torr^{-1}$ (Machin, 1967). Using this coefficient and the approximate surface area (0.26 cm^2) and thickness (0.01 mm) of a *Gastrocopta armifera* shell suggests that, if the pupillid shell were similarly permeable, EWL through the shell alone would amount to 1.86 mg day^{-1} or about 34% day^{-1} at VPD = 23.8 torr (25°C, 0% RH). Measured *total* loss in these conditions is two orders of magnitude less (Table 3). Little is known of the factors limiting shell permeability to water and comparisons of shell structure between pupillids and helicids would therefore be of interest.

Most EWL from dormant helicid snails occurs at the shell aperture (Machin, 1975). Besides the impermeability of the shell, it is evident that physiological mechanisms for water conservation such as the intracellular water barrier of the mantle collar (Machin, 1975), and reduced oxygen consumption and lung ventilation during dormancy (Barnhart, 1986), must be highly developed in pupillids. Active *Gastrocopta armifera* reduced EWL 92% by retracting into the shell (from 89.9 to 7.2 mg day^{-1}; Table 4) but loss declined over 400 fold further during dormancy (to 16.5 μg day^{-1}; Table 2).

Survival During Dormancy

Although *Gastrocopta armifera* typically survived only about 2.5 months of dormancy at 25°C, 0% RH in this study, several individuals left undisturbed survived at least 9 months in these conditions (Barnhart, unpublished data). Undisturbed snails maintain lower metabolic rate and EWL than those periodically weighed (Schmidt-Nielsen *et al.*, 1971; Machin, 1975). Maximum weight loss observed in *G. armifera* before death (30–50%) is similar to tolerable weight losses reported for several larger species of shelled land snails and lower than those of shell-less pulmonate slugs (table 13 of Machin, 1975). Unlike slugs (Prior, 1985), pupillids have apparently not developed unusual ability to tolerate water loss.

Effects of Temperature, Humidity and Activity

Lack of proportionality between VPD and EWL in dormant pupillids indicates that temperature and humidity affect EWL by mechanisms other than by simply altering the physical driving force for evaporation. Skewed distributions and high variance of EWL among individuals (Figure 1, Table 3) suggest occasional arousal from dormancy and consequent EWL. Metabolic rate and arousal are influenced by temperature and humidity (Horne, 1973; Herreid & Rokitka, 1976; Riddle, 1975). Lower EWL in the second month of dormancy (Table 1) may reflect increased commitment to dormancy and fewer incidents of arousal.

Unlike some arthropods, which absorb water vapor from subsaturated air (Edney, 1977), snails must contact a moist surface in order to rehydrate (Prior, 1985). Because of their unusual susceptibility to water loss during activity, pupillids should be particularly constrained to arouse from dormancy and emerge from the shell only when free water is available to replace evaporative loss. In *Gastrocopta procera*, 10 min of crawling at 60% RH results in water loss

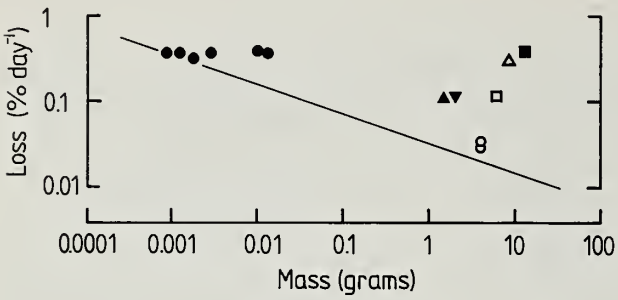

Figure 2

Evaporative water loss of dormant land snails vs. whole body mass. Rates are percent total body water per day. Closed circles are data from the present study (Table 2). Open circles, *Sphincterochila boissieri* (upper, MACHIN, 1967; lower, SCHMIDT-NIELSEN *et al.*, 1971). Closed triangle, *Helicella virgata* (POMEROY, 1968). Closed inverted triangle, *Otala lactea,* and open triangle, *Helix aspersa* (MACHIN, 1967). Open square, *Rabdotus schiedeanus* (RIDDLE, 1975). Closed square, *Caracolus caracolus* (HEATWOLE & HEATWOLE, 1978). All measurements were made at 20–25°C and 0–20% RH. Line shows the predicted loss rate of the smallest species extrapolated to larger size, assuming constant surface area-specific loss. The smallest species apparently have the lowest area-specific loss rates (see Discussion).

equivalent to 124 days of dormancy. Given this constraint, it appears that pupillids may be a particularly interesting group in which to investigate behavioral responses to the wide variety of environmental cues that affect arousal from dormancy in pulmonate snails.

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Differences in the Frequencies of Several Shell Characters in the Clam *Donax variabilis* Around Cape Hatteras, North Carolina

by

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Abstract. Samples of the coquina clam, *Donax variabilis,* were collected from four sites around Cape Hatteras, North Carolina. The extensive polymorphism in these clams was subdivided into variation for five characters: background color, presence or absence of colored umbo, rays, and rings on the exterior of the shell, and presence or absence of interior pigment. For each clam, the shell was measured for length and scored for the five characters. The sites were highly heterogeneous both for shell lengths and for the frequencies of the qualitative characters. Each site presented a unique combination of shell lengths and morph frequencies, and neither mean shell length nor the frequencies of any of the five characters showed a consistent pattern of differences among the five sites. Most probably, *D. variabilis* in the Hatteras region forms disjunct populations that initiate at different times or respond to extremely local environmental conditions or both. Any future studies must examine changes in *Donax* over very short distances, preferably over at least a year's time.

INTRODUCTION

The coquina clam, *Donax variabilis* Say, 1822 (Bivalvia: Donacidae), has long been noted for the great variety of shell colors and markings found within any one of its populations. The polymorphism has been little studied, however, while considerable attention has been paid to the ecology and behavior of this organism (for an extensive bibliography see NELSON, 1985). Clams of the genus *Donax* possess an ability—to live intertidally on sandy, wave swept beaches—that is so unusual that much attention has been given to the behavioral adaptations that allow this genus to follow the tide in and out, remaining in the wash zone (TURNER & BELDING, 1957; LEBER, 1982). At the same time, WADE's (1967, 1968) conjecture that differences in diet are responsible for the variation in shell colors and markings, combined with the great difficulty of making Mendelian paired matings of bivalves, has caused students of ecological genetics to avoid the genus. Only CHANLEY (1969) has succeeded in spawning *D. variabilis* in the laboratory, and he used mass, not controlled, matings. However, evidence for the simple genetic basis of shell polymorphisms in other bivalve mollusks is becoming available (CHANLEY, 1961; INNES & HALEY, 1977; ADAMKEWICZ & CASTAGNA, 1988). It is reasonable to begin a detailed study of the polymorphism in *Donax,* using analogies to known genetic systems until attempts at genetic analysis are successful.

Three workers (SMITH, 1975; MIKKELSEN, 1978; SCHNEIDER, 1982) have examined the polymorphism under the assumption that it is genetic and might be maintained by selection. Each of the three suggests that apostatic selection (CLARKE, 1962) or reflexive selection (MOMENT, 1962) exerted by visual predators might explain the wide variety encountered. ALLEN (1988) and OWEN & WHITELEY (1988) have raised the issue again in discussing the enormous amount of variation in the genus *Donax.* However, a thorough study of the problem has not yet been undertaken. The most immediate need is for a systematic description of the variation present. When considered as unitary morphs, the shells are so varied that no two individuals appear to be alike, and this polymorphism needs to be reduced, perhaps by subdividing it into several independently varying traits. Two additional needs are a test of the stability of frequencies over time at one site and an examination of frequencies at a single time over an extensive geographic area.

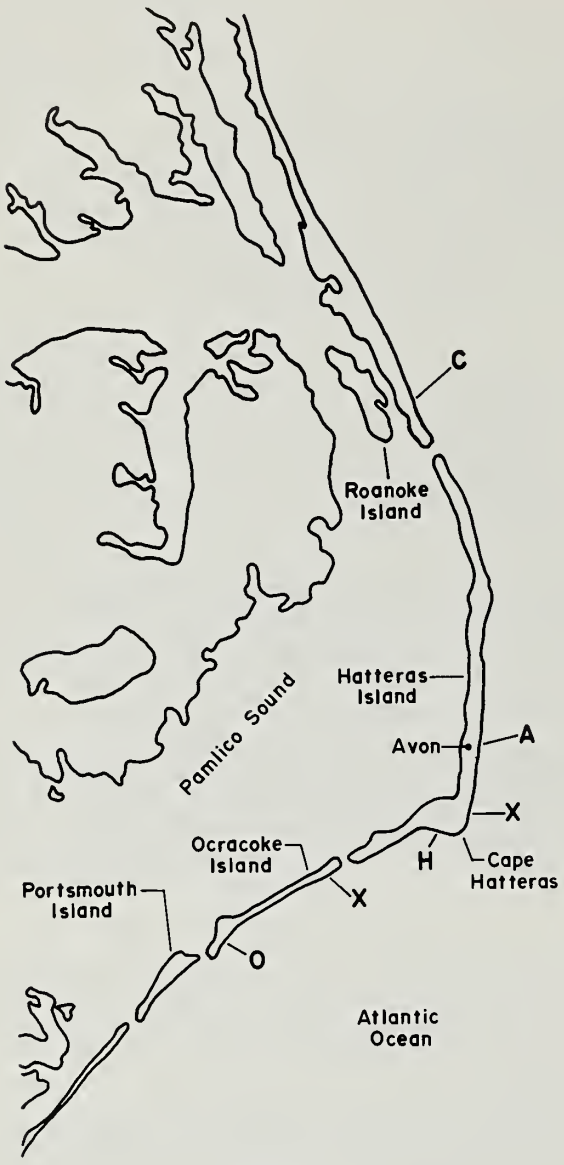

Figure 1

Map of North Carolina's outer banks showing the collection sites from north to south as follows: C = Coquina Beach, A = Avon, H = Hatteras, and O = Okracoke. At the sites marked X, no specimens of *Donax variabilis* were found.

MIKKELSEN (1978) has made a beginning on all three points with his work on *Donax variabilis* in Florida, where he followed one Atlantic and one Gulf population over a six-month period. While he reports substantial differences in shell sizes and in frequencies of various morphs between the two sites, he does not report having tested frequencies of morphs over time in either location nor does he report any data on size of shell by morph. Mikkelsen has also chosen to use an objective, quantitative measure of shell color, the Munsel Color System (KELLY & JUDD, 1955). This choice does permit an objective designation of the overall impression given by a shell, but it makes recognition of individual, subsidiary traits difficult. The quantitative standard also blurs the distinction between qualitative (perhaps genetics) and quantitative (perhaps environmental) differences. The present paper uses instead SMITH's (1975) approach of designating qualitative classes in the hope that a careful separation of the different aspects of color and pattern will serve as a guide to genetic experiments. To promote standardization of classification, the author has placed in the collection of the U.S. Museum of Natural History a set of labeled shells that exemplify the variants described here. The present study also determines both the length of the shell and the value of each character for each clam collected. When recruitment is episodic, as it is in *D. variabilis*, these data sometimes permit the detection of differential growth and (or) survival among morphs and may provide information about the agents that affect the polymorphism.

With these changes of method, the present study attempts to extend our knowledge of the polymorphism by dissecting it into several components and then examining their frequencies in samples taken at a single time across what is known to be a major biogeographical boundary. If differences in geographical location were to be correlated with changes in frequencies among morphs, this would be evidence that the polymorphism in *Donax variabilis* is maintained at least in part by environmental selective agents. Because Cape Hatteras, North Carolina, represents a dividing line both for water circulation patterns and for the northern and southern forms of many marine organisms, it is a promising location in which to examine the frequencies of shell colors and patterns. In addition, two unpublished studies suggest that Hatteras might be an area of rapid changes in frequency. The frequencies of various shell morphs differ significantly in collections from Virginia and Florida, and sharp changes in the frequencies of alleles for the gene encoding leucine aminopeptidase occur around Cape Hatteras. The purpose of this paper is to report shell lengths and the frequencies of several shell characters in samples taken around Cape Hatteras in October of 1986.

MATERIALS AND METHODS

Collections

Donax variabilis inhabits the wash zone of sandy beaches from Delaware to Florida and around the Gulf of Mexico. The species occurs sporadically but can reach a density of 15,619 per m^2 (NELSON, 1985) in some locations. For simplicity, the clams from a single site are referred to as a population, but it is not known whether the individuals at a given site are in fact an interbreeding population or whether they are simply an aggregation of individuals from more than one source (NELSON, 1985). The animals de-

scribed here were collected on 12 and 13 October of 1986 from four sites along the outer banks of North Carolina (shown in Figure 1). Of six sites visited, only four had aggregations of *Donax* and these four were sampled as described below. The sites covered a linear distance of approximately 114 km: 64 km between Coquina and Avon, 10 km between Avon and Hatteras, and 40 km between Hatteras and Okracoke. They were chosen primarily for accessibility and secondarily for regular spacing around the cape. No effort was made to quantify the characteristics of the beach sites. The four sites did differ in their slopes (with Hatteras steepest) and in the amount of broken shell present, but, by subjective judgement, the substrate colors were alike.

Each site was visited during daylight within one and one-half hours of a low tide. The wash zone was examined and, when *Donax* were sighted, the beach to a depth of about 4 cm was shoveled into a sieve and washed to remove the sand. The mesh of the sieve was 3 mm with a diagonal opening of 4.2 mm and, while the sieve retained an unknown proportion of animals below 4 mm, it clearly did not retain all of them, nor could it trap very small individuals. To obtain an unbiased sample of all sizes would require taking cores of the beach. For purposes of this study, emphasis was placed on obtaining a large sample of adult animals in a short period of time. Similarly, no attempt was made to estimate population densities. Rather, collecting effort was adjusted to produce approximately equal sample sizes. Extra effort did not achieve a sample from Avon equal to those from the other sites, indicating that the population there was indeed less dense.

Once a sample had been sieved, the retained broken shells and living clams were placed in bags with ethyl alcohol (which does not affect the shell or its colors) and transported back to the laboratory where the *Donax* were separated from the debris. Each shell was cleaned, its length was measured with calipers to the nearest 0.1 mm, and its color and pattern elements were recorded both for interior and exterior surfaces. Every animal counted had clearly been collected alive and its two valves were always kept together. The data were later analyzed with the SAS statistical package, primarily with the procedures "FREQUENCY" and "ANOVA," executed on a VAX 8800 computer at George Mason University.

Shell Characters

For their studies, Smith (1975), Mikkelsen (1978), and Schneider (1982) classified shells primarily by their overall appearance with some markings, especially rays, also noted. The present study does not use this approach. The colors and markings are distinctive enough to be treated as qualitative variables and they can be scored consistently by eye. Furthermore, the overall appearance of the shell is determined by the interaction of what appear to be several independent characters. While the names chosen for these characters might vary among investigators, the categories themselves are easy to recognize. Most of these correpond to characters recognized by Mikkelsen and these are noted where appropriate.

At least four pigments of unknown chemistry account for the colors seen in these Cape Hatteras samples of *Donax variabilis*. These colors are yellow, brown, red, and purple. A fifth color, white, is most probably the absence of any pigment. Each of these pigments is characteristic of different pattern elements on the shell. For the purposes of this study, the multiplicity of colors and patterns seen in *D. variabilis* were reduced to the following five characters:

Background. The background color of the shell can be either yellow or white (uncolored). Occasionally a shell may appear to be another color, but this effect is generally attributable to the presence of other pigments applied in one of several patterns over the background color which cause reflected colors. No third background color such as reported by Mikkelsen (1978, in Sanibel, Florida) was observed. However, in Florida *Donax* are even more colorful and variable than they are in North Carolina.

Umbo. The umbo region of the shell can be unmarked, in which case it shows the background color of the shell, or it can be covered with a spot of color, either purple or red. This character is the same as the "P-Umbo" of Mikkelsen (1978).

Rays. The shell can be marked with rays radiating from the umbo toward the growing lip. In some cases the shell has two or three purple rays that do not extend all the way to the lip. This is the P-J-R or P-juvenile pattern of Mikkelsen (1978). In other cases, the rays are red or brown rather than purple and extend from umbo to lip much like the pattern in tellinid clams. Although in the present study both of these patterns are called "rays," they are almost certainly different traits. The incomplete rays are always purple and few in number while the complete rays are never purple and are usually more than three in number.

Rings. Periods of faster and slower growth produce rings in the shell independent of any pigmentation. When pigment is secreted periodically, the shell can be marked with rings of color that run parallel to the growing lip. If the rings were either white or yellow, they were discounted as part of the normal growth process. If the rings were purple or red, the shell was counted as ringed. Brown rings were never seen. The distinction between the systems for rings and rays is demonstrated by rare shells that have both brown rays and blue rings.

Inside. The interior of the shell can be unpigmented. Conversely, it can be marked with purple pigment that covers (a) only the posterior half of the shell (toward the foot, the pattern designated "half") or (b) the entire inner surface of the shell ("entire"). One of the principal difficulties in interpreting earlier studies is the authors' omission of any mention of color inside the shell. This pigment can often be seen through the shell of the living

Table 1

Frequencies of various shell characters of *Donax variabilis* by collection site. The last column gives the probability (P) associated with a χ^2 test of homogeneity for the frequencies of variants for the character among the four sites.

Shell character	Collection sites: Coquina (n = 479)	Avon (n = 167)	Hatteras (n = 494)	Okracoke (n = 411)	P
Background					
Yellow	0.487	0.473	0.453	0.372	0.004
White	0.513	0.527	0.547	0.628	
Umbo					
Unmarked	0.771	0.826	0.879	0.698	0.0001
Purple	0.129	0.096	0.095	0.095	
Red	0.100	0.078	0.026	0.207	
Rays					
Absent	0.263	0.174	0.366	0.292	0.0001
P-juvenile	0.601	0.712	0.496	0.589	
Brown/red	0.136	0.114	0.138	0.119	
Rings					
Absent	0.722	0.731	0.567	0.514	0.0001
Purple/red	0.278	0.269	0.433	0.486	
Inside					
Uncolored	0.566	0.605	0.591	0.611	0.0001
Half	0.133	0.042	0.045	0.083	
Entire	0.301	0.353	0.364	0.306	

animal thus giving a bluish tint to a white animal or a muddy brown tint to a yellow one.

RESULTS

Frequencies of Shell Characters

Comparison of the four samples clearly demonstrates that aggregations of *Donax variabilis* are not uniform around Cape Hatteras, while the same comparison refutes the idea that regular north-south clines occur for most characters. Table 1 shows the frequencies by site for the variants of each shell character. When the frequencies for any one character are compared over all sites with a χ^2 test, the results show a significant deviation from homogeneity in every instance (probability always less than 0.01). Not only do the sites differ in the frequencies of these variants, the pattern of these differences among sites is not the same for all the characters. The character "background" exhibits a consistent decrease in the frequency of yellow from north to south at the same time that the characters "umbo" and "rays" show the northern and southernmost sites to be most alike. For the character "rings," the two northernmost sites form a pair in contrast to the two southernmost locations, while the character "inside" shows no obvious pattern at all. Because the frequencies of these variants change significantly over rather short distances and because that pattern of change is different for each character, each site has a distinctive suite of frequencies.

While the combination of these patterns and colors does lead to a large number of morphs, the five shell characteristics do not always occur independently of one another. Table 2 summarizes the results of pairwise χ^2 tests of independence for each possible pair of characters at each sampling site. Despite the potential for spurious significance when large numbers (40) of tests are performed, the results are clear. For any pair, either the χ^2 values had probabilities at or above the 0.05 level for all sites, in which case the pair was considered to be independent, or else the values were at or below the 0.001 level for at least three of the sites, in which case the pair was considered to be associated.

Background color of the shell is independent of markings on the shell with one exception, the presence of a colored umbo. At each site, regardless of frequencies, red umbo appears on shells with yellow background color far more often (overall frequency 0.145) than on shells with white background (overall frequency 0.067). Purple umbo (overall frequencies of 0.101 and 0.109 on yellow and white backgrounds respectively) does not show this pattern. The cause of the association is unknown, but it cannot be forced by the pigment system because it is not absolute. A shell can have either background color with either umbo color.

The presence of rays of any kind is independent of the presence of rings, and one does find shells with both brown rays and clearly developed purple rings. The other five pairs of shell markings show significant associations with

Table 2

Results for χ^2 tests of independence performed on each pair of *Donax variabilis* shell characters for each site. To compensate for the multiple testing, a significance level of alpha = 0.001 was used. If an association is marked with **, it was significant at this level in each of the four samples. A mark of * indicates significance in three of the four samples. χ^2 values for the other pairs only sporadically reached the 0.05 level of probability.

Character pair	Independent	Pattern of occurrence
Background & umbo	no**	red ubmo occurs more frequently on yellow background than on white
Background & rays	yes	random
Background & rings	yes	random
Background & inside	yes	random
Umbo & rays	no**	pigmented umbo and rays of any kind not usually present together
Umbo & rings	no**	shells with purple umbo are more likely to have blue rings
Umbo & inside	no**	shells with purple umbo usually have pigmented insides
Rays & rings	yes	random
Rays & inside	no*	no consistent pattern
Rings & inside	no**	shells with purple rings are more likely to have pigmented insides

one another and four of these associations appear to have the same basis. If any one purple marking is present, the chance that another purple mark will be present increases. In particular, when a purple umbo is present, the inside of the shell is much more likely to be either half or entirely pigmented than when the umbo is not colored. The overall frequency of shells with interior pigment is 0.411, while among shells with purple umbo it is 0.820 and among shells with unpigmented umbo it is 0.302. The one association that does not follow the pattern of one purple marking increasing the likelihood of another is that between pigmented umbo and rays. When the umbo is pigmented, rays of any kind are present less frequently (0.599) than when the umbo is pigmented (0.826). The cause of these associations is not known, but presumably the ability to produce purple pigment is a prerequisite for the expression of any pattern involving purple pigment.

Shell Characters and Length

Figure 2 shows the distribution of shell lengths at each site. Clearly, the four samples are heterogeneous for shell length just as they are for the frequencies of the shell characters. Each mean is significantly different from those

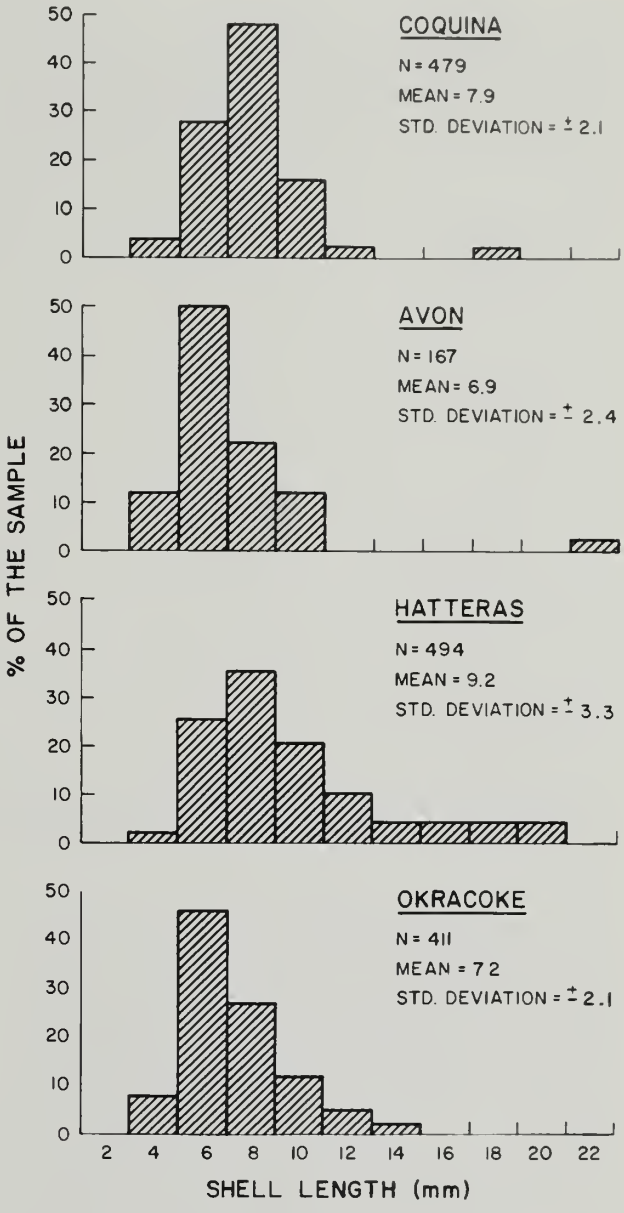

Figure 2

Distribution of shell lengths of *Donax variabilis* at the four collection sites.

at the adjacent sites (ANOVA with Duncan's Multiple-Range Test, $P < 0.05$) although the means for Avon and Okracoke do not differ significantly. The truncation of the distribution toward 2 mm shell length undoubtedly reflects the fact that the collection technique did not reliably detect smaller animals. Even with this distortion, one can see that the Hatteras sample contains a far greater proportion of larger animals than any other site and that Avon has the smallest clams.

Table 3

Mean shell length in millimeters (with standard error) for the variants of each *Donax variabilis* shell character by collection site. Asterisks signify that adjacent means for a given site are significantly different at the 0.05 level either using a two-tailed *t*-test for two means or Duncan's multiple-range test for three.

	Collection sites			
Shell character	Coquina (n = 479)	Avon (n = 167)	Hatteras (n = 494)	Okracoke (n = 411)
Background				
Yellow	8.2 (±0.15)*	7.3 (±0.27)	9.5 (±0.23)	7.4 (±0.17)
White	7.5 (±0.11)*	6.6 (±0.25)	9.0 (±0.19)	7.2 (±0.13)
Umbo				
Uncolored	7.6 (±0.11)*	6.9 (±0.21)	9.3 (±0.16)	7.3 (±0.13)
Purple	8.5 (±0.20)	5.9 (±0.33)	8.4 (±0.40)	7.6 (±0.33)
Red	8.6 (±0.21)	8.2 (±0.37)*	9.2 (±1.03)	7.0 (±0.16)
Rays				
Absent	8.2 (±0.15)	7.8 (±0.81)	9.6 (±0.28)	7.4 (±0.21)
P-juvenile	7.9 (±0.13)*	6.8 (±0.15)	9.4 (±0.23)	7.2 (±0.15)
Brown/red	7.2 (±0.22)*	6.0 (±0.35)	8.6 (±0.36)	7.0 (±0.23)
Rings				
Absent	7.6 (±0.11)*	6.7 (±0.19)*	8.7 (±0.18)*	6.7 (±0.14)*
Purple/red	8.6 (±0.17)*	7.5 (±0.43)*	9.9 (±0.24)*	7.8 (±0.15)*
Inside†				
Uncolored	7.6 (±0.13)	6.6 (±0.17)	8.9 (±0.17)	6.9 (±0.12)
Half	8.0 (±0.16)	12.1 (±2.61)*	10.4 (±1.00)	8.3 (±0.40)*
Entire	8.2 (±0.17)	6.9 (±0.21)	9.6 (±0.26)	7.6 (±0.19)

† An analysis of variance shows that the effect of inside coloration on shell length is significant at each site. In each case, the largest and smallest means differ significantly and, where marked*, adjacent means differ.

Mean lengths of the shell for the morphs of each character are given in Table 3. For each character at each site, an analysis of variance tested the hypothesis that shell length was influenced by which morph was present. The results of these ANOVAs were not always significant, and the presence or absence of a colored umbo appears to be unrelated to shell length. For inside pigmentation, background color, rays, and rings, however, one morph is consistently larger than another even though the effect is often not significant. Shells with pigmented interiors are always larger than shells with no pigment. Shells with yellow ground color are always larger than shells with white ground color (probably the absence of pigment). Shells with no rays are consistently larger than shells with the p-juvenile pattern which are in turn always larger than shells with brown rays, although the effect is significant only at the Coquina Beach site.

DISCUSSION

Unless genetic data become available, one cannot be certain of the correct interpretation for the color and pattern variants in *Donax variabilis*. However, one can argue by analogy with other molluscan systems that these variants are quite likely to have simple Mendelian bases. In the land snail *Cepaea* (Cain *et al.*, 1960), the coloration of the spire, white or pink, is determined by a single gene and this situation may well be analogous to the pigmentation of the umbo in *D. variabilis*. Three examples are available from other marine bivalves: (1) the presence of rays on the shell, a pattern very similar to brown/red rays in *D. variabilis,* is determined by a single gene with incomplete dominance in the clam *Mercenaria mercenaria* (Chanley, 1961), (2) the background shell color, white versus yellow or orange, is controlled by a single gene in the scallop *Argopecten irradians* (Adamkewicz & Castagna, 1988), and (3) the difference between purple and brown shell color in the mussel *Mytilus edulis* is also determined by a single gene (Innes & Haley, 1977). Such examples of genetic control over shell characters make it unlikely that similar phenotypes in *D. variabilis* are environmentally determined as Wade (1968) originally suggested. The significant differences in frequencies of these characters among sites probably reflect differences in gene frequencies, while the independence of the various components of the polymorphism suggests that each component may be responding to different forces. The immediate challenge is to discover why these differences exist and what the causes might be.

The heterogeneity of samples over relatively short distances is surprising, particularly in a marine organism with a planktonic larval stage, and shows a clear need for

studies over still shorter distances. All previous work has suggested that difference among sites would show broad geographic patterns. Owen & Whitely (1988) have noted a relationship in the genus *Donax* between amount of variation and latitude, with the more colorful species occurring in the south, and the same pattern holds within the species *D. variabilis* where populations are much more colorful in Florida than in Virginia. However, in *D. variabilis,* even background color, which does show a consistent decrease in the frequency of yellow from north to south, must be even more heterogeneous over distance than appears from the present study. Mikkelsen (1978) reports that the proportion of yellow at Indialantic Beach on the Atlantic coast of Florida is 62%, which means that the frequency of yellow must rise substantially somewhere south of Okracoke. Red markings of any kind become more frequent as one moves south along Hatteras, but this trend appears not to continue south to Florida where red is much more common on the Gulf coast than on the Atlantic. Assuming that the basis for these differences is variation in allele frequencies along the coast, the observed heterogeneity must have one of two causes. Either the differences represent random variation in neutral traits or else they are the result of natural selection which differs in intensity, direction, or both from site to site.

Each interpretation has both advantages and difficulties. If genetic drift produced the observed frequencies, then the breeding populations of *Donax variabilis* must be much smaller and more localized than one would expect either from their observed numbers on beaches or from their mode of reproduction. Such a population structure is not impossible, but it implies that only a small fraction of the adults (perhaps unseen in offshore areas) ever reproduces successfully. If natural selection produced the observed differences in frequencies, then the beach habitat along the North Carolina coast is more heterogeneous, on a finer scale, than appears at first examination. Selection by water temperature and (or) salinity, factors that vary on a large scale, should produce regular clines, not the heterogeneous patterns observed. The visual predators observed by Smith (1975) and Schneider (1982) have large foraging ranges and do not vary in population density over such short distances. If crypsis and visual predation are involved, then the beaches must differ more in color and (or) composition than is apparent by casual examination. Smith (1975) proposes that young *Donax* resemble individual grains of sand and that one must examine a beach on that scale in order to detect crypsis. His suggestion that the frequencies of different colors among the grains of sand on a beach influence crypsis should be investigated further. A final possibility, related to Smith's proposal, is that selection is apostatic, or negatively frequency dependent (Clarke, 1962; Moment, 1962). If a morph's fitness depends on its frequency, then clams in all of the samples might be responding to the same forces while populations were in different stages of a complex and shifting equilibrium.

Understanding the cause of heterogeneity in shell lengths will be a key to understanding the forces acting on the polymorphism. Because the ages of these clams are unknown, the data cannot distinguish between the effects of growth rate and age on length of the shell. However, the life cycle of *Donax variabilis* in only one year long (Nelson, 1985) and shell length reflects at least approximate age. Three possibilities exist. (1) The clams in any given sample may indeed be members of a single, transient breeding population. Differences in sizes among sites would be the result of foundings at different times. This model is consistent with the observation that *Donax* occurs sporadically on many beaches. (2) The clams at any one site might, as Mikkelsen (1985) believes possible, be a mixture of individuals washed in from several different breeding populations. (3) The heterogeneity of shell lengths might result from different growing conditions at each site. In this view, animals that began growth at the same time would reach larger sizes in areas that had superior conditions. Wade (1967, 1968) has proposed this explanation for the substantial size differences he found on different beaches.

Any of the three interpretations leads to the conclusion that *Donax variabilis* is highly subdivided, and the models differ only in whether the animals in one sample are regarded as members of a breeding population. The evidence is insufficient but favors either the first or third interpretation. An examination of the shell lengths at each site shows a unimodal distribution typical of a single population of mixed ages. It seems unlikely that a mixture of animals from several sources would produce the same distribution. The distinction is a critical one for study of the polymorphism because, if the mixture model should prove to be correct, frequencies of morphs in any one sample would be meaningless and the polymorphism could not be understood until the source populations were located and studied. If the varying growth rate model is correct, then selection based on resource availability becomes more probable, while if the isolated population model is correct, drift based on founder effects becomes more likely. Clearly, any future studies must be conducted with fine scale sampling and attention to demographic parameters.

The data on mean shell length for each character do show that heterogeneity of shell lengths among sites cannot itself be the cause of heterogeneity in the frequencies of the shell characters. For shell length to influence morph frequency, size would have to affect either the ability of the clam to form the character or the ability of the investigator to detect it. The data do not support either possibility. Background color of the shell does not change during the life of an individual and the smallest clams can be recognized as either white or yellow. Furthermore, the highest and lowest frequencies of yellow do not occur at the two sites most different in mean length. Similarly, the colored umbo is equally distinct at all shell sizes and its frequency at a site is unrelated to mean shell length at that site. The rayed patterns are actually more difficult to see on small shells and, if the appearance or detection of rays were causally related to shell size, one would expect

the mean size to be larger for rayed shells than for unrayed. In fact, the reverse is true. The relationship between shell length and the presence of rings also might depend on shell length, with individuals required to reach a certain size before secreting the first ring. However, the data do not support even this hypothesis because the frequency of rings is highest in the sample (Okracoke) with the second smallest mean length.

The most interesting associations with shell length are those of background color and inside pigmentation. Not only is the mean for yellow shells always larger than the mean for white, but the presence of pigment inside the shell always yields shells with a larger mean than does absence of pigment. Oddly, the shells with only half the inside covered with pigment have a larger mean than those that are fully colored. It is possible either that darker shells grow faster, perhaps by absorbing more heat, or that darker shells survive better. The present data will not distinguish between differences in survival and differences in growth rate, but MITTON (1977) has shown a definite association between shell color and survival at high temperatures in the mussel *Mytilus edulis*. To distinguish between the possibilities, any future study must follow frequencies over time at a single site.

In summary, the data show that aggregations of *Donax variabilis* are highly heterogeneous over relatively short distances both for shell length and for the frequencies of five polymorphic traits. Each site presented a unique combination of shell lengths and morph frequencies and neither mean shell length nor the frequencies of any of the five characters showed a consistent pattern of change among the five sites. The variations in frequency of the shell characters do not show a common pattern and the variations in size and in frequency cannot be causally related. Most probably, *Donax variabilis* in the Hatteras region forms disjunct populations that initiate at different times and (or) respond to extremely local environmental conditions. Any future studies must examine differences in *Donax* over very short distances preferably over at least a year's time.

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Larval and Early Postlarval Development of *Macoma mitchelli* Dall (Bivalvia: Tellinidae)

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Abstract. Specimens of *Macoma mitchelli* were spawned and the larvae and juveniles reared (ca.9‰ and 23°C) for 67 days. Recently spawned eggs measured 59 ± 2.3 μm. Straight-hinge larvae 70–80 μm long developed within 20 h of spawning, and pediveliger larvae settled into sand by day 6 or day 7 after spawning (approximate size range at settlement: 160–205 μm). A short exhalant siphon developed by day 15 (juvenile size range: 240–340 μm), but an inhalant siphon did not appear until some time between day 41 and day 52 (size range: 390–910 μm). Shell-hinge structure included a series of small denticles during larval developmental stages, development of an umbo at a shell length of 120–150 μm, appearance of a prominent ligament pit at a shell length of approximately 170 μm, and development of articulating cardinal teeth in animals larger than about 210 μm.

INTRODUCTION

Macoma mitchelli Dall, 1895 (=*Macoma phenax* Dall, 1900) is a burrowing tellinid bivalve found in meso-polyhaline waters of Chesapeake Bay, where it attains a maximum size of about 16 mm (Blundon & Kennedy, 1982b; Hines & Comtois, 1985). The species has not been much studied, and most reports consist of a listing of its presence in samples collected during regional surveys of benthic biota along the Atlantic and Gulf Coasts of the United States (*e.g.*, Parker, 1959; Tenore, 1972; Redding & Cory, 1975). In Chesapeake Bay, *M. mitchelli* may be abundant in soft sediments (Pfitzenmeyer & Drobeck, 1963; Hines & Comtois, 1985), with fluctuations in abundance apparently linked to seasonal predation (Holland *et al.*, 1980; Blundon & Kennedy, 1982a, b). Newly settled spat and small juveniles (<5 mm) have been found in benthic samples throughout the year (Shaw, 1965; Blundon & Kennedy, 1982b).

We report here the results of laboratory spawning and rearing of *Macoma mitchelli*, including information on larval hinge structures. Such information should be useful to those seeking to identify larvae and juveniles in planktonic or benthic samples (Lutz *et al.*, 1982).

MATERIALS AND METHODS

Adult bivalves were collected in the summer (ca.9‰ and 23°C) from the Choptank River, Maryland, offshore from Horn Point Environmental Laboratories (38°36'N;

76°09'W), and were held in bowls in running, cooled (18°C) river water. A number of attempts were made to spawn these adults by placing groups in clean bowls containing 1-μm-filtered river water (ca.9‰) and held in a water bath in which temperatures were varied periodically from about 18°C to 25°C. Water samples were collected and examined microscopically both before and after spawning occurred. After spawning occurred and we judged that a quantity of sperm had been released that was sufficient to fertilize the eggs present, the water in the bowls was washed through an 88-μm screen to remove debris and into a 30-L plastic garbage can containing 1-μm-filtered river water (ca. 9‰). Larvae were cultured at about 23°C in this container until they were ready to metamorphose.

Algal food (Tahitian *Isochrysis* sp. and *Chlorella* sp.) was provided daily (1:30 mix). The culture water was renewed every second day by retaining the larvae on screens, discarding the old culture water, and adding new 1-μm-filtered river water. A few milliliters of water from the larval culture were sampled daily, and larvae were examined microscopically until metamorphosis occurred. For 24 to 30 larvae, we measured shell length (maximum anteroposterior distance, μm) and height (maximum dorsoventral distance, μm) to the nearest 5 μm under a microscope with a calibrated ocular micrometer. When the larvae became pediveligers, they were placed in 1.5-L glass bowls, with sand on the bottom. After they had metamorphosed, juveniles continued to be held in bowls of sand, and measurements of length × height were continued irregularly for about two months; the juveniles were fed algae and examined until many were ca. 4 mm long. In addition to measuring the size of 10–25 juveniles each observation day, we made notes on their behavior and on changes in siphonal anatomy.

Samples of larvae and juveniles were preserved in 70% ethanol to provide material for photomicrographs of external shell morphology. Material for scanning electron microscopy was placed in distilled water for about 30 min and then preserved in 95% ethanol (Lutz *et al.,* 1982). Thereafter, specimens were taken from the preservative, rinsed in distilled water, and placed in a 5% solution of sodium hypochlorite for about 10 min. The resulting separated shell valves were rinsed in distilled water, mounted on silver tape, coated with ca. 600 Å of gold-palladium, and examined under an ETEC Autoscan scanning electron microscope. During scanning electron microscopic documentation of internal views of left and right valves, consistency of shell orientation was maintained by maneuvering each specimen so that four points (each 90° apart) along the shell edge were in the same plane of focus at about 30,000× (Lutz *et al.,* 1982). Shell dimensions were determined by comparison with standard grids photographed at the same magnification as each shell specimen.

RESULTS

Two attempts at spawning these clams were successful, with one producing few larvae and the other being more productive. Results from both attempts are consolidated for this report, but all shell measurements and photographs are those of animals from the more successful second spawning.

Adult males extended their exhalant siphon about three to four times the length of the clam during spawning, and muscular waves ran along the length of the siphon. Sperm were released in intermittent, smokelike puffs, although occasionally a steady stream of sperm was produced for a few seconds. The length of the head of a typical sperm was 5–10 μm, with a maximum width of 1–2 μm. Sperm tails were "pigtailed" in shape; their length was not determined.

Egg release was not observed, but eggs were found in water samples pipetted from the bowls within 90 min of stimulating clams by varying the temperature. Average egg size at this time was 59 ± 2.3 μm ($n = 25$). Eggs that had been in the presence of sperm for some time were seen to be surrounded by a sperm "aura," with the sperm apparently trapped in clear material (fertilization membrane?) about one-half the diameter of the egg away from its surface.

Straight-hinge larvae developed within 20 h after spawning, when larvae were 70–80 μm long (*e.g.,* Figure 1F). An apical flagellum was present and was retained until metamorphosis. A slight saddle shape in the hinge region, somewhat similar to the shell of the larger *Lyonsia hyalina* (Chanley & Castagna, 1966), was noted in 48-h larvae (80–85 μm). The "D shape" began to be lost by 94 h after spawning (95–115 μm), with a more oval shape becoming apparent (Figures 1B, 2). The umbo had become more prominent by 118 h (120–150 μm), and larval shape was more circular than oval. The anterior end of the shell was more prominent by 144 h (130–165 μm) and continued to develop as shown in Figures 1C–F, 3. As development continued, the broadly rounded umbo gradually became knobby (Figure 3) (Chanley & Andrews, 1971). A club-shaped foot was apparent in many larvae by 144 h, but it was used actively by only a few larvae >160 μm, whereas by 168 h (155–190 μm) the foot was active in many larvae. By day 6 (first batch of larvae) or day 7 (second batch), young clams responded to the presence of sand by digging. By this time most had lost their velum. Eyespots were not noted at any time during development. The approximate size range at metamorphosis was 160 μm (the size of the smallest larva noted to have an active foot) to 205 μm (the largest larva with an active foot and a functioning velum).

Metamorphosed animals (spat) tended to have particles adhering to the shell and were sometimes found to stick together (see also Webb, 1986). Larger animals had reddish shells (see also Chanley, 1969). By day 15 (240–340 μm), many juveniles had a short exhalant siphon that could be protruded from the shell and from which particles were occasionally expelled. Particles were also expelled from the opening of the shell below the siphon. No inhalant siphon was present, and particles were drawn into the mantle cavity at the end opposite the siphon end. Juveniles were examined on day 25 (300–400 μm), day 33 (350–

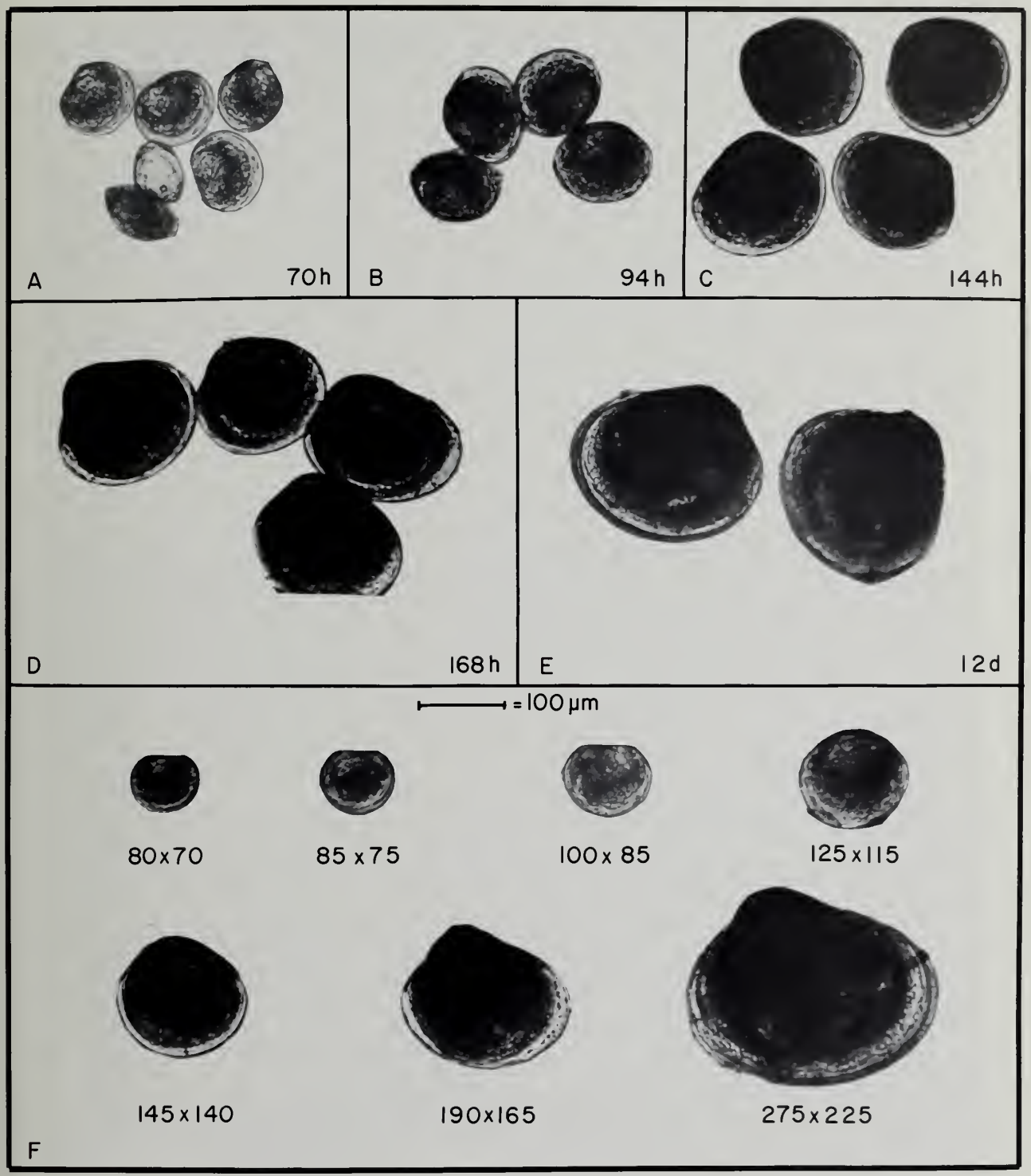

Figure 1

Photomicrographs of *Macoma mitchelli* larvae and postlarvae. A–E. Grouped clams ranging from 70 hours (h) to 12 days (d) old. F. Individual clams of representative lengths, with anterior end to right. Measurements (µm) are length × height. Scale line applies to all animals, including grouped clams.

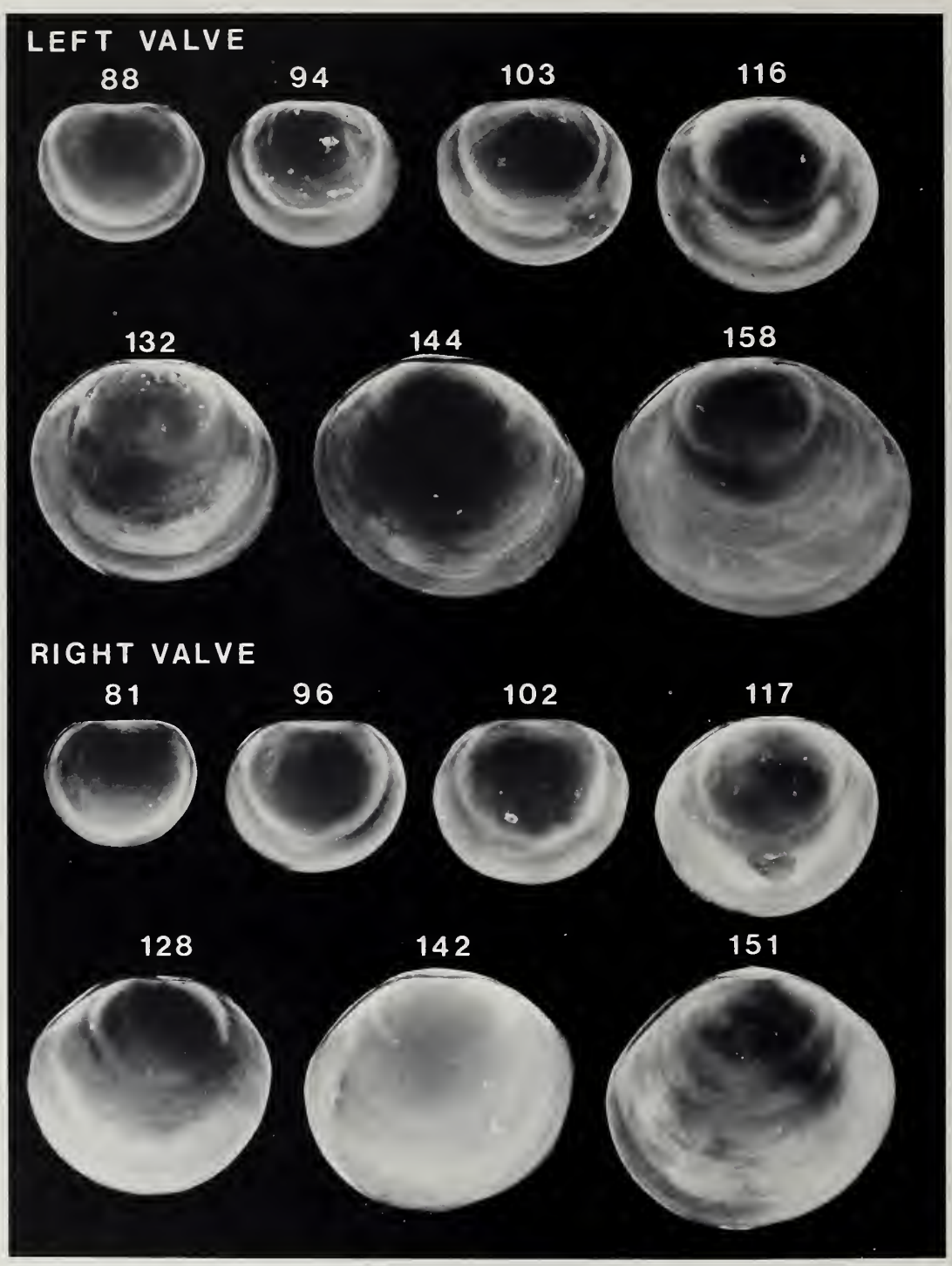

Figure 2

Scanning electron micrographs of interiors of disarticulated shell valves of *Macoma mitchelli* larvae. Numbers are shell length (μm).

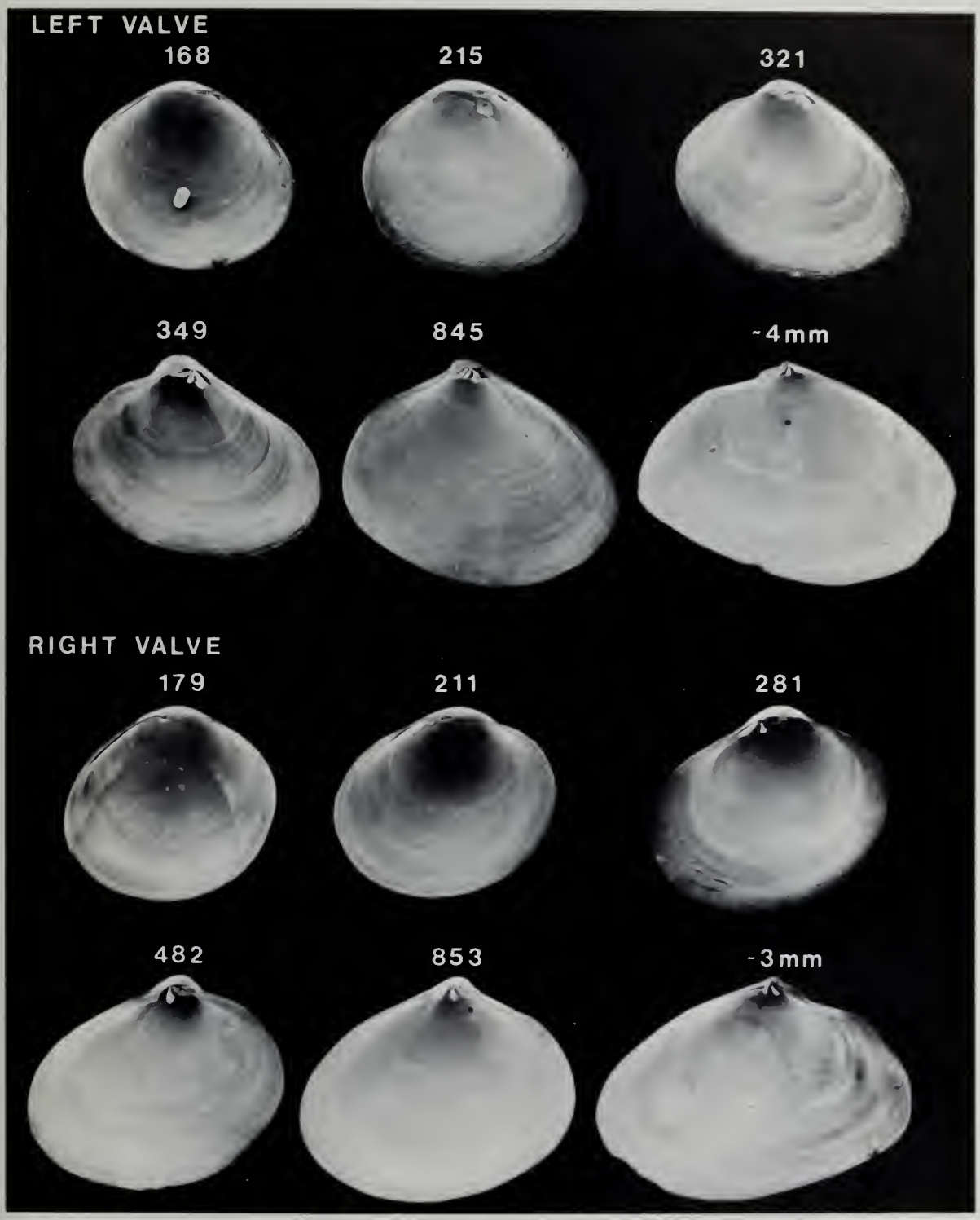

Figure 3

Scanning electron micrographs of interiors of disarticulated shell valves of *Macoma mitchelli* postlarvae. Numbers are shell length (μm).

Figure 4

Scanning electron micrograph of the exterior surface of an early postlarval valve (length, ca. 275 μm) of *Macoma mitchelli*. Arrow marks transition from commarginal to cancellate sculpture.

Figure 5

Scanning electron micrograph of the exterior surface of a shell of a 41-day-old *Macoma mitchelli* (length, ca. 600 μm).

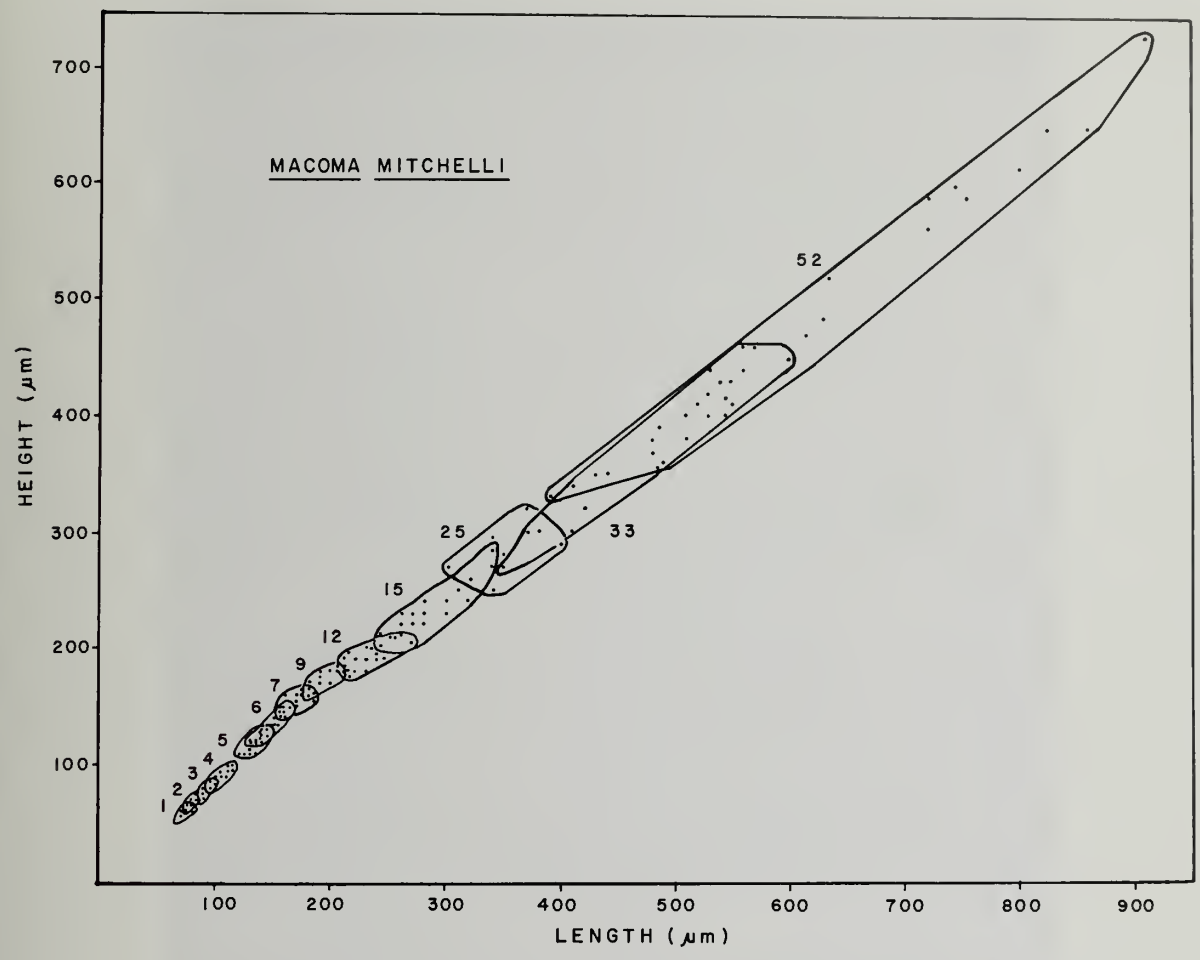

Figure 6

Length-height relationships (days 1–52) for *Macoma mitchelli* larvae and juveniles, to show increased size scatter over time. Metamorphosis occurred by day 7. Points may represent measurements on more than one animal.

600 μm), and day 41 (370–620 μm), but no inhalant siphon was noticed until day 52 (390–910 μm). All but the smallest clams had paired siphons by day 67. However, at no time was the inhalant siphon seen in use. Particles continued to enter the shell cavity ventrally, even in spat as large as 3.4 mm (day 67).

Examination of exterior shell morphology of early postlarval specimens showed an abrupt transition from commarginal to cancellate sculpture (Figure 4) at an average length of 193.8 ± 5.7 μm (range: 183–201 μm; n = 15). The postlarval shells were found to have distinct external commarginal ridges (*e.g.*, Figure 5; see also WEBB, 1986) when observed by light microscope on day 41 (shell length: 370–620 μm; ridge numbers: 4–11). Over 40 ridges were visible in the shells of clams >3.4 mm long (day 67). By day 67, most spat had attained the typical adult shape of *Macoma mitchelli* and possessed a wedge-shaped foot.

Separate linear regressions were fitted to data on length-height relationships for days 1–7 ($y = 1.6 + 0.90x$; $r^2 = 0.90$; $n = 159$, where y = height and x = length) and days 9–67 ($y = 23.2 + 0.74x$; $r^2 = 0.99$; $n = 120$) because there appeared to be a break in the curves between days 7 and 9 (Figure 6). This period of time encompassed the end of pelagic development and the beginning of benthic existence. Figure 6 also demonstrates increasing disparities in size among clams of the same age as time passed. By day 67, some animals were longer than 4.2 mm, while others were as small as 580 μm long.

Examination of larval and postlarval shell-hinge structures of the specimens shown in Figures 7 and 8 revealed numerous, small denticles on the larval hinge. A prominent ligament pit appeared at a shell length of approximately 170 μm; subsequent development of cardinal teeth on the anterior region of the postlarval hinge began when shells were approximately 210 μm long (Figure 8). After metamorphosis, the ligament pit of juveniles enlarged, as did

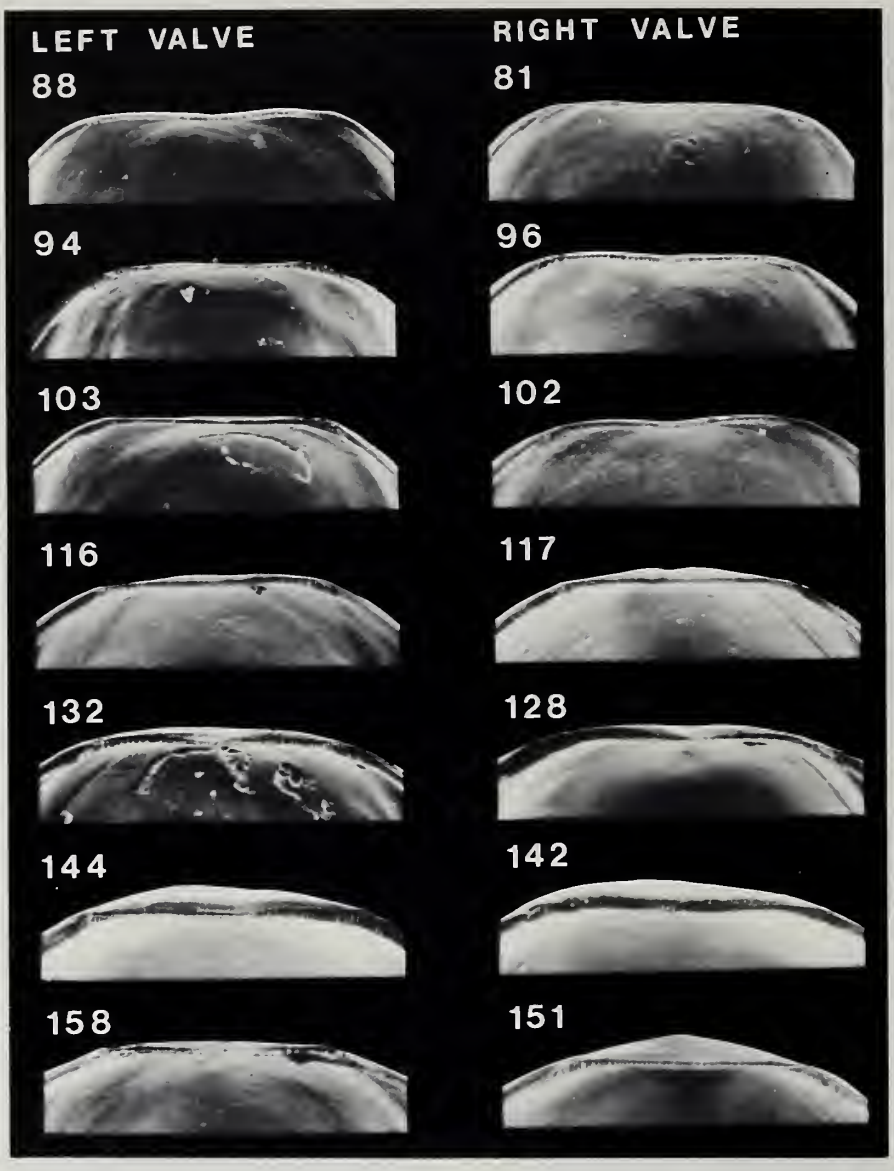

Figure 7

Scanning electron micrographs of the hinge apparatus of larval valves pictured in Figure 2. Numbers are shell length (μm).

the cardinal teeth on each valve (Figure 8). The articulating nature of these cardinal teeth is shown clearly in a comparison of left and right hinge structures of the larger animals pictured (Figure 8). At a shell length of approximately 3 to 4 mm, cardinal teeth had differentiated into laminate and bifid forms (Figure 8).

DISCUSSION

Although our objective was to rear and describe larval and postlarval stages of *Macoma mitchelli*, some of our observations have relevance to results of other studies. *Macoma mitchelli* developed and metamorphosed quickly compared with other species studied on the east coast of North America, most of which are reported to require 10 or more days to reach metamorphosis (Loosanoff & Davis, 1963; Chanley & Andrews, 1971). However, a few east coast species are known to develop about as quickly as *M. mitchelli*. At 20°C, *Laevicardium mortoni* metamorphosed by eight days after fertilization (Loosanoff & Davis, 1963). *Rangia cuneata* (an oligohaline species found in Chesapeake Bay) began to set at a size range of 160–175 μm after seven days at 22–24.4°C (Chanley, 1965). *Lyonsia hyalina* (Chanley & Castagna, 1966) began meta-

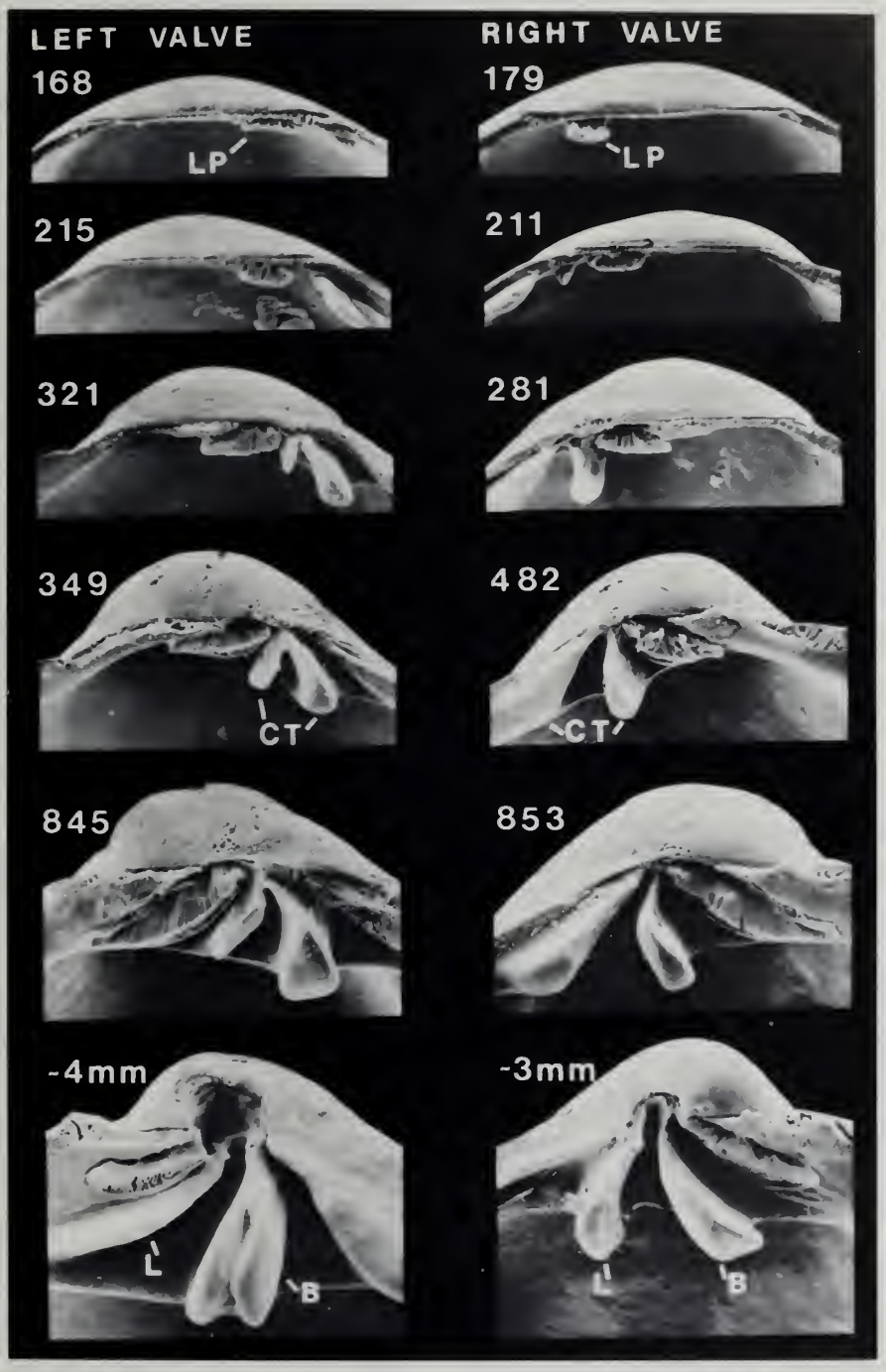

Figure 8

Scanning electron micrographs of the hinge apparatus of postlarval valves pictured in Figure 3. Numbers are shell length (μm). CT, cardinal teeth; LP, ligament pit; B, bifid cardinal tooth; L, laminate cardinal tooth.

morphosis three days (18–22°C) after fertilization at sizes ranging from 155 to 175 μm (see also CAMPOS & RAMORINO [1981] for data on rapid settlement of the lyonsiid *Entodesma cuneata* in Chile). *Macoma balthica* in Chesapeake Bay can also settle in less than one week at about 21°C (personal observations).

During development, the external morphology of *Macoma mitchelli* (pronounced anterior end, knobby umbo,

commarginal ridges) resembled that of other tellinids (*e.g.*, CHANLEY & ANDREWS, 1971; WEBB, 1986). However, the external morphology of juvenile *M. mitchelli* does not resemble that of juvenile *M. balthica,* the other common tellinid in central and upper Chesapeake Bay, in that the latter retains the more circular outline of the adults (personal observations). Internally, the ligament pit in *M. mitchelli* (Figure 8) did not appear to develop until larvae had reached the size range for metamorphosis, supporting the suggestion by LUTZ & HIDU (1979) that such structures are postlarval features. Similarly, as postulated for tellinacean larvae by CHANLEY (1969) and shown for postlarval *Tellina fabula* by WEBB (1986), development of the cardinal teeth was most noticeable after metamorphosis (Figure 8; postlarvae >210 μm). While a ligament pit formed early in metamorphosis (visible in specimens with a shell length as small as 168 μm [Figure 8]), dissoconch cancellate sculpture was not apparent until a size of 183–201 μm.

Limited information is available on morphological development of soft-body parts of young bivalves, such as development of the siphon. The exhalant siphon seemed to develop more slowly in *Macoma mitchelli* than in the tellinid *Abra alba* (AABEL, 1983) in which the siphon can extend beyond the shell margin at metamorphosis. Such behavior was not noted in *M. mitchelli* until day 15 after spawning. As in *A. alba,* newly settled *M. mitchelli* had no inhalant siphon. The inhalant siphon develops in *A. alba* at the end of the third month after settlement (at 10°C), at a shell length of about 1 mm (AABEL, 1983). In *M. mitchelli,* an inhalant siphon was not noticed on day 41 but was apparent in some clams at day 52 (animals <1 mm), with most clams possessing paired protrusible siphons on day 67. As in juvenile *A. alba,* in the absence of a functioning inhalant siphon, currents established by individual *M. mitchelli* brought suspended particles in through the ventral opening of the shell. Because no inhalant siphon was observed to be in use during our observations of juvenile *M. mitchelli,* we cannot provide information to compare with the changed method of particle uptake found in *A. alba* after the inhalant siphon comes into use. However, we suspect that feeding behavior would be similar in *M. mitchelli.*

ACKNOWLEDGMENTS

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Depth of Occurrence and Partial Chemical Composition of a Giant Squid, *Architeuthis*, off Southern California

by

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Abstract. The tentacle of a giant squid, *Architeuthis* sp., was collected at a depth between 500 and 600 m in deep water off the coast of southern California. This capture provides the first direct evidence of habitat depth for *Architeuthis*. Chemical composition analyses of the tentacle reveal a protein and water balance that suggests a relatively strong swimming capability, in conjunction with buoyancy provided by ammonium ion concentration.

INTRODUCTION

Giant squids of the genus *Architeuthis* have been known since the middle of the last century, but information about their natural history has been even more elusive than the animals themselves. Most of what is known about them has been derived from dead or moribund specimens found stranded near shore or floating in the open sea, and from beaks and other tissues found amid the stomach contents of sperm whales and fishes (Clarke, 1966; Roper & Boss, 1982; Boyle, 1986). As a result, the scope of our knowledge of these enigmatic giants includes primarily: geographical distribution records, morphology, some indications of trophic relationships, a confused taxonomy, and a great deal of speculation. While the majority of *Architeuthis* specimens have been found in the North Atlantic and the western North Pacific, the genus has a circumglobal distribution (Roper & Boss, 1982). Records from the eastern Pacific are sparse. Off California, *Architeuthis* beaks have been found in the stomachs of sperm whales (Fiscus & Rice, 1974) and an albacore (Pinkas *et al.*, 1971), but there has been almost no direct evidence from captures, sightings, or strandings. Direct evidence is also lacking on the vertical distribution of *Architeuthis*, and the data suggesting either near-benthic or midwater modes of life are equivocal (Clarke & Merrett, 1972; Roper & Young, 1972; Clarke & McLeod, 1974). High concentrations of ammonium in the body fluids of *Architeuthis*, particularly the arms, indicate that they are almost neutrally buoyant (Clarke *et al.*, 1979).

MATERIALS AND METHODS

The present report is based on an *Architeuthis* tentacle collected by a messenger-activated, RMT-8 midwater trawl (Clarke, 1969) in October of 1980, at 32°28′30″N, 120°15′48″W, off southern California. Bottom depth at the sampling locality was 4400 m and the temperature at the sampling depth was 6.1°C. The tentacle was caught by the towing and releasing bridles of the trawl, during a discrete-depth haul that sampled the water column between 500 and 600 m, at a speed of 2.5 kts. While the tentacle was collected by the hardware on the outside of the net mouth, its position between the bridles was such that it could only have been taken at the depths where the trawl mouth was open.

After capture the tentacle was deep frozen and the tentacle club was deposited in the collection of the Santa Barbara Museum of Natural History (Accession No. B-1257). Chemical analyses were conducted on thawed tentacle tissues and on the liquid drained from them, according to the methods described by Bailey & Robison (1986). Ammonia concentrations were measured colorimetrically using flow-injection analysis (Johnson *et al.*, 1985). To provide equivalent data for comparison, tentacle or arm samples from three other cephalopods were also

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Figure 1

Oral surface of the tentacular club of *Architeuthis,* immediately after capture. At this point the tissues still responded to mechanical stimulation.

analyzed. *Vampyroteuthis infernalis* Chun, 1903, is an archaic, cosmopolitan, midwater cephalopod, with a soft gelatinous body that appears to be ill-suited for strong swimming (PICKFORD, 1946; MARSHALL, 1979). *Bathyteuthis berryi* Roper, 1968, is the local species of a widely distributed bathypelagic genus (ROPER, 1969) that is believed to use both ammonium ions and a lipid-rich liver to attain near neutral buoyancy (DENTON & GILPIN-BROWN, 1973; CLARKE *et al.,* 1979). Individuals of *Bathyteuthis* spp. are also believed to be sluggish swimmers (MARSHALL, 1979). In contrast, the market squid *Loligo opalescens* Berry, 1911, is an active, strong-swimming epipelagic species (YOUNG, 1972) that is considerably denser than seawater.

RESULTS

The tentacle, which measured 4.27 m in length, had obviously been wrenched from a living squid; the tissue was still elastic, the suckers contracted and gripped when they were touched, and the chromatophores contracted when rubbed. The length of the tentacular club (including carpus) was 41.5 cm, that of the dactylus was 15.3 cm, and the manus length was 24.5 cm (Figure 1). The diameter of the largest sucker on the manus was 1.85 cm (Figure 2). The depth of capture was about 150 m below the main sonic scattering layer (at 12 kHz), which marked the core of the midwater fauna at 1400 h. In terms of individual biomass, the principal species in the trawl catch were: *Vampyroteuthis infernalis*; the mysid *Gnathophausia ingens* Dohrn, 1870, and the fishes *Borostomias panamensis* Regan & Trewavas, 1930, *Chauliodus macouni* Bean, 1890, *Idiacanthus antrostomus* Gilbert, 1890, *Scopelengys tristis* Alcock, 1892, and *Stenobrachius leucopsarus* (Eigenmann & Eigenmann, 1890).

Results of the chemical composition analyses are presented in Table 1. The *Architeuthis* and *Loligo* tentacles showed relatively high protein concentrations and low water content. While lipid levels were low in all of the samples, *Architeuthis* and *Loligo* also had the highest lipid concentrations. Ash weight was significantly higher in *Vampyroteuthis* than in the three squids. The highest ammonium levels occurred in the liquid expressed from the *Architeuthis* tentacle and in the tentacle tissue from *Bathyteuthis.* The composite ammonium values for these two species were an order of magnitude greater than in *Loligo,* and two orders of magnitude larger than in *Vampyroteuthis.* These am-

Figure 2

Suckers on the manus show the tetraserial armature pattern of the Architeuthidae, and their serrated chitinous rings. Black marks on the rule are 1 mm apart.

Table 1

Results from chemical composition analyses of samples from four cephalopods. The constituents, except water and ammonium, are presened as mean percentages of wet weight (% ww). CHO = carbohydrate. Tentacle values for *Architeuthis* and *Bathyteuthis* represent tissues from which the liquid had been expressed. Data for *Vampyroteuthis* and *Loligo* represent composite values of liquid and flesh. Standard deviations are in parentheses.

Species	Sample	% H_2O	Ash wt (% ww)	Protein (% ww)	CHO (% ww)	Lipid (% ww)	NH_4^+ (mM)
Architeuthis sp.	tentacle	80.19	1.85	12.12	0.02	1.59	182.59
	liquid	98.41	0.31	0.13	0	0	314.03
	composite	86.12	1.35	8.34	0.01	1.09	225.40
		(4.75)	(0.06)	(1.75)	(0.02)	(0.26)	(21.43)
Bathyteuthis berryi	tentacle	87.24	2.48	8.54	0	1.00	262.74
	liquid	97.73	0.73	0.48	0	0.03	141.99
	composite	92.85	1.54	4.23	0	0.48	198.19
		(0.40)	(0.40)	(0.13)		(0.01)	(4.15)
Vampyroteuthis infernalis	arm	94.03	2.41	1.84	0.06	0.54	3.22
		(0.17)	(0.18)	(0.00)	(0.03)	(0.08)	(0.31)
Loligo opalescens	tentacle	84.53	1.58	9.64	0.04	1.47	21.21
		(0.99)	(0.90)	(0.92)	(0.00)	(0.03)	(1.99)

monium values for *Architeuthis* are similar to the arm and mantle values reported by CLARKE *et al.* (1979).

DISCUSSION

Obviously, the capture of a single tentacle can yield only a limited amount of data about *Architeuthis*. Nevertheless, the dearth of knowledge about giant squids is such that even a tentacle can provide useful new information. Most significant is the fact that it was reliably collected at mesopelagic depths, thus providing the first direct evidence of habitat depth for *Architeuthis*. Previously available evidence from squid predators has suggested that juveniles may live in the water column (ROPER & YOUNG, 1972), whereas adults may live on or near the bottom at depths around 1000 m (ROPER & BOSS, 1982). In the present case, while the specimen was clearly captured in midwater, the site is within 30 km of the Patton Escarpment which rises abruptly from a depth of 3500 m to less than 2000 m.

While opinions differ, *Architeuthis* has been generally assumed to be a relatively weak swimmer because of poorly developed musculature, loose structural morphology, and the low oxygen carrying capacity of its blood (ROBSON, 1933; ROPER & BOSS, 1982; BRIX, 1983). However, analyses of chemical composition patterns in midwater fishes and crustaceans have shown that high levels of protein in conjunction with low water content are correlated with higher locomotory capabilities and metabolic activity levels (CHILDRESS & NYGAARD, 1974; CHILDRESS *et al.*, 1980; BAILEY & ROBISON, 1986). If the same is true of midwater cephalopods, which are subject to most of the same selective factors, then giant squids may be relatively good swimmers. In terms of their protein and water content, the *Architeuthis* samples were much more akin to *Loligo* than to the watery, soft-bodied *Vampyroteuthis* and *Bathyteuthis*. The composition of the *Architeuthis* samples differed from *Loligo* primarily in their higher ammonium content. A better evaluation of swimming potential would be based on comparison of mantle tissues.

The present data set is based on only a portion of a single *Architeuthis,* and it should not be extrapolated to represent whole body composition or species-wide depth habits. Unfortunately, much of what we know about this genus is based on such bits and pieces. The resolution of questions about the depth range, activity and ecology of *Architeuthis* will require a considerably better data base than we have managed to acquire over the last century.

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The Publications and Taxa of the Reverend Joseph Rowell (1820–1918)

by

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Abstract. Joseph Rowell (1820–1918) was a clergyman who collected mollusks in Panama and California. He described five species, and type material has been located for each of them.

Joseph Rowell, seventh in descent from a Thomas Rowell who emigrated to America from England in 1638, was born in Cornish, New Hampshire, 22 April 1820. At the age of 21, he left this village to attend Kimball Union Academy at Meriden, New Hampshire, earning his own way. Upon completion of his courses, he built a boat, shot the rapids on the Connecticut River, and made his way to Yale College in New Haven, where he graduated in 1848. Deciding on a career in the ministry, he attended the Union Theological Seminary in New York, completing his work there in 1851 (FERRIER, 1918; WEBSTER, 1918; KURTZ, 1939).

He soon accepted a call to become chaplain to Panama under the joint auspices of the American Seamen's Friend Society and the American and Foreign Christian Union. "Panama," he told them, "is a pestilential hole, and it will be hard to find a good man to go there. I am tough, and I can stand the climate if anyone can. I will go." So, armed with a letter of introduction to the U.S. consul in Panama from Secretary of State Daniel Webster, he went.

He remained in Panama from 1851 to 1858. There, in 1852, he married Hannah Cummings, the daughter of a New England minister. In 1852, he had his first son, Joseph Cummings Rowell, who later became the librarian of the University of California at Berkeley.

It was in Panama that he began making a shell collection. On 22 December 1855, James G. Cooper, on his way back to the East Coast from the Pacific Railroad Exploring Expedition to the Pacific Northwest, first met Rowell (COAN, 1982:59). He wrote in his diary:

> "Visited Mr. Rowell, American missionary, who has a good collection of about 100 species made during four years past. He says bulimi can be got only at Taboga, and several other kinds about those and the Pearl Islands only. He has a dredge, which I can get."[1]

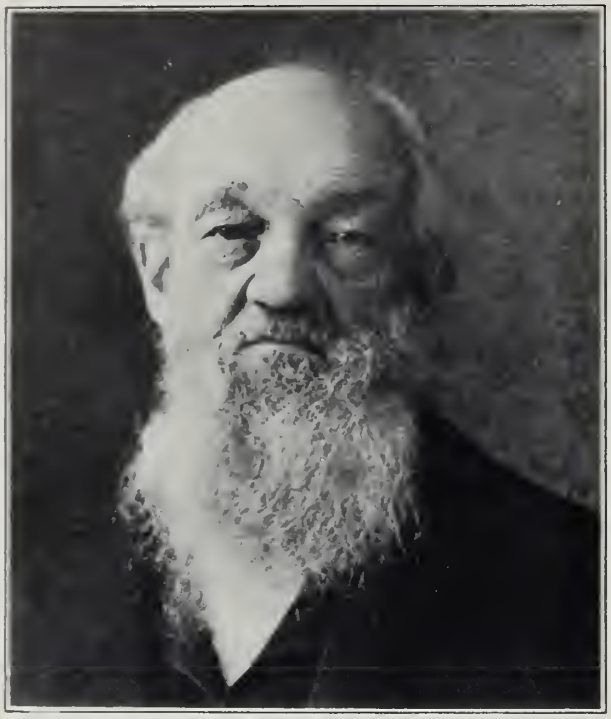
In July 1858, the Rowell family moved to San Francisco. Within a few weeks, he began to preach to sailors at the Seamen's Bethel Church. In 1867, he built what became the world famous Mariner's Church on the corner of Sacramento and Drumm streets. According to a biographer, "Sailors in all the four corners of the world knew this Mariner's Church and told grateful and admiring tales of its wise and generous and tireless chaplain. Its altar, fashioned like the bow of a sailing ship, was described on all the seven seas" (KURTZ, 1939:6).

Rowell continued mollusk collecting in California, and he regularly sent material to the Smithsonian Institution (CARPENTER, 1864:631, 1865:278–282). Some species were acquired among oysters imported to San Francisco from Acapulco, Mexico. HAINES (1886:40) described him as "one of the best informed conchologists upon this coast, and whose collection of shells, comprising many species, has but two or three rivals among private collections in America." Keep described Rowell thus: "A clergyman of San Francisco, who has described several new species, and who has collected a very fine cabinet of shells" (KEEP, 1887:220).

The only other glimpse we have of Rowell by other malacologists came late in his life, when Stillman Berry visited him on 15 April 1914. There are two accounts of this visit, a manuscript prepared in the 1940s, which was later greatly shortened when published (BERRY, 1948)[2],

[1] Journal for 1855–1856. Smithsonian Inst. Archives, Rec. Unit 7067, Cooper Papers, 1853–1870.

[2] The draft MS is in the SBMNH.



Joseph Rowell, 1820–1918

and the oral history materials that Donald R. Shasky and I prepared on Stillman Berry in 1980[3]:

> "Well, it happened in the spring . . . 1914. . . . I discovered that Joseph Rowell was living in San Francisco, still alive. . . . So, I took my last opportunity one afternoon to go out Market Street to as near where he lived as possible, then I walked to his house. He wasn't far from the old Mission. . . . And he was *very* cordial. . . . He was an old man, but his mind was good, and if I had had more time, I would have learned a great deal more than I did. He was a close personal friend of Thomas Bridges, the nephew . . . of Hugh Cuming [and] who spent his last years in Oakland. . . . He still had quite a bit of his collection. He gave me sets of [two] Californian things he had described—*Vertigo californica* . . . and *Gundlachia californica*—and a book he thought I would like . . . , the second edition to the *Conchologists First Book* by Edgar Allan Poe, a very rare item[4]. . . . Its first owner, whose autograph is on the flyleaf, was the earliest malacologist in my native state of Maine, J. W. Chickering of Portland, and he gave the book to Rowell."

Sometime after Rowell's death on 5 June 1918, his collection went to the University of California at Berkeley. There, however, I have been able to locate type material of only two of his five taxa. Fortunately, between the specimens he gave to Stillman Berry, now housed at the Santa Barbara Museum of Natural History, and Rowell lots that reached other institutions, there is available type material of each of his new taxa, which are listed below.

Each entry in the following list consists of: (1) the name as originally proposed, with date, and page and figure numbers (keyed to the Literature Cited); (2) the type locality, including refinements based on other information; (3) the number of specimens, if indicated in the original publication; (4) type material, including museum numbers, type status, and number of specimens (in parentheses); and (5) remarks, including current taxonomic assignment. References are provided in the Literature Cited for all taxa mentioned, except for senior synonyms of Rowell's taxa. It also includes references to two other Rowell works on mollusks not containing new taxa. The following abbreviations are used: ANSP, Academy of Natural Sciences, Philadelphia; CAS, California Academy of Sciences, San Francisco; SBMNH, Santa Barbara Museum of Natural History; UCMP, University of California at Berkeley, Museum of Paleontology; UMMZ, University of Michigan, Museum of Zoology.

ACKNOWLEDGMENTS

I am grateful to the curators of several museums for helping to locate Rowell specimens: Academy of Natural Sciences (Arthur Bogan); California Academy of Sciences (Michael Kellogg); Santa Barbara Museum of Natural History (Paul Scott); United States National Museum of Natural History (Diane Bohmhauer); and University of California, Berkeley, Museum of Paleontology (David Lindberg). Advice about some of Rowell's taxa was provided by Barry Roth. Eric Wilson helped track down some obscure references. The portrait of Rowell is reproduced courtesy of The Bancroft Library at the University of California, Berkeley.

LIST OF TAXA

angelicum, Pisidium—ROWELL, 1867:353. Angel Island, San Francisco Co., California; several specimens.

Type material—UCMP 10617, syntypes (36 pairs, 3 valves) (Loc. 7195); Carnegie Museum 3840, syntype (1).

Remarks—BURCH (1975:57) listed this as a *nomen nudum,* crediting the name to HERRINGTON (1954:101). However, is it clearly made available by Rowell. Herrington said that the Carnegie Museum specimen is actually a crustacean. However, the lot at UCMP contains pisidiid clams (Lindberg, *in litt.,* 16 June 1988).

californica, Gundlachia—ROWELL, 1863:21–22; fig. 5. Feather River at Marysville, Yuba Co., California; Rowell; more than 50 specimens, on water plants in clear stagnant pools.

[3] The original tapes of these interviews are in the American Malacological Union Archives at the ANSP. Transcripts of these tapes are available in several institutions, including the ANSP, SBMNH, and USNM. The quotation is rearranged for clarity.

[4] Concerning this book, see KEEN (1936).

Type material—SBMNH 35010, lectotype (BERRY, 1948:16) (formerly SSB 4501; not deposited in CAS as CAS 8044, as stated by Berry); SBMNH 35011, paralectotypes (2); UMMZ 102011, "holotype" (BEQUAERT & MILLER, 1973:211).

Remarks—*Laevapex* (*Ferrissia*) *californica* (Rowell), according to BEQUAERT & MILLER (1973:211); synonym of *Ferrissia fragilis* (Tryon, 1863), according to BASCH (1963:435–440) and BURCH & TOTTENHAM (1980:215; fig. 764), but Rowell's paper was published in May, Tryon's paper was published in July, and a third synonym introduced the same year, *Gundlachia meekiana* STIMPSON (1863:250–251; figs. 2, 3), was published in December. *Ferrissia californica* (Rowell), according to TAYLOR (1981:161).

californica, Pupa—ROWELL, 1861:287. San Francisco, San Francisco Co., California; a considerable number; Rowell.

Type material—SBMNH 35008, lectotype (BERRY, 1948:16) (formerly SSB 3337; not deposited in CAS as CAS 8043, as stated by Berry); SBMNH 35009, paralectotypes (6) (none deposited in SDMNH, as stated by Berry); ANSP 59392, paralectotypes (16), including the two figured by PILSBRY (1948:996–997; figs. 533-1, 2).

Remarks—*Vertigo californica* (Rowell), according to PILSBRY (1948).

rubicunda, Epiphragmophora exarata var.—ROWELL, 1902: 52. Occidental (2 specimens) and Freestone (quite a number), Sonoma Co., California; Rowell.

Type material—ANSP 83367, lectotype (BAKER, 1962: 18) from Freestone; ANSP 371035, paralectotype (1) from Freestone; ANSP 83366, paralectotype (1) from Occidental.

Remarks—Synonym of *Helminthoglypta arrosa holderiana* (Cooper, 1875), according to PILSBRY (1939:110–111; fig. 52b).

soquela, Helix (*Epiphragmophora*) *sequoicola*—ROWELL, 1905:41–42. Midway between Soquel Creek and "Skyland," Santa Cruz Co., California; Rowell.

Type material—ANSP 89785, syntype (1); UCMP 38215, syntype (1) (Loc. 1008); CAS 036248, syntype (1).

Remarks—Synonym of *Helminthoglypta sequoicola* (Cooper, 1866), according to PILSBRY (1939:140–141; fig. 70b).

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A Revision of the Western Atlantic Recent Species of the Genus *Monostiolum* Dall, 1904, and *Bailya* (*Parabailya*) New Subgenus (Gastropoda: Buccinidae)

by

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Abstract. Western Atlantic species of the buccinid genus *Monostiolum* Dall, 1904, are reviewed: *M. tessellatum* (Reeve, 1844) from Bermuda and most of the Caribbean; *M.* ***auratum*** Watters & Finlay, sp. nov., from Puerto Rico and the Lesser Antilles; and *M.* ***rosewateri*** Watters & Finlay, sp. nov., from Barbados. The well-known name *swifti* (Tryon, 1881) is shown to be a junior synonym of *tessellatum*. *Caducifer* (*Monostiolum*) *weberi* (Watters, 1983) is removed from *Monostiolum* and selected as the type species of *Bailya* (***Parabailya***) Watters & Finlay, subgen. nov.

INTRODUCTION

The conglomeration of taxa once known as "tritons" has confounded malacologists since the days of Linné. What was once considered a group of conchologically similar species has now been allocated to the muricids, cancellariids, cymatiids, and the buccinids, among others, on the basis of protoconch, radular, and anatomical features. Many unstudied taxa may remain taxonomically misplaced. Perhaps the most misunderstood of these groups is the Buccinidae, which encompasses species showing a range of form and diversity seldom seen in other families of marine gastropods. The species herein referred to the buccinid genus *Monostiolum* Dall, 1904, have had a complicated taxonomic history that includes erroneous or absent locality data for types and incongruous systematic associations. The most common species in this group in the western Atlantic, still referred to as *Colubraria swifti,* has two earlier names and does not belong to *Colubraria.*

Although often associated with *Caducifer* Dall, 1904, the relationship of *Monostiolum* to the New World genus *Bailya* M. Smith, 1944, has largely gone unnoticed. *Bailya* is conchologically similar to *Monostiolum* and shows many of the features of the genus. *Bailya* (***Parabailya***), new subgenus herein described, appears to be derived from *Bailya,* based upon the evidence of fossil species of *Monostiolum* and *Bailya.*

ABBREVIATIONS

AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; BM(NH), British Museum (Natural History), London; DMNH, Delaware Museum of Natural History, Greenville; FURG, Fundaçao Universidade do Rio Grande, Museu Oceanográfico, Sao Paulo, Brazil; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.

SYSTEMATICS

Family Buccinidae Rafinesque, 1815

Subfamily Pisaniinae Tryon, 1880

Genus *Monostiolum* Dall, 1904

Colubraria (*Monostiolum*) Dall, 1904:136.
Pisania (*Monostiolum*) Dall: Fulton, 1936:8.
Monostiolum (*Monostiolum*) Dall: Ponder, 1972:255.
Caducifer (*Monostiolum*) Dall: Cernohorsky, 1975:196.

Type species: *Triton swifti* Tryon, 1881, by original designation.

Description: Shell small, fusiform, with a single terminal varix. Protoconch of 1½ smooth nuclear whorls. Generally 7 postnuclear whorls. Sculptured with spiral cords, threads, and axial ribs which may become weaker on the body whorl. Outer lip with weak denticles, parietal callus partially adherent with a single denticle delimiting the anal canal. Columella distinctly bent at the siphonal canal. Siphonal canal short, open, and weakly set off from body whorl.

Operculum phylliform with a subterminal nucleus.

Radula rachiglossate; central tooth with three cusps, lateral teeth with three medially curving cusps each, the most distal being the largest.

Remarks: Dall (1904:136) erected both *Monostiolum* and *Caducifer* as sections under *Colubraria* Schumacher, 1817, in the Aquillidae. He separated *Caducifer* from *Monostiolum* solely on the basis of the former having ¼ of its spire "self-amputated." It is possible that the presence of a decollated spire may be a characteristic of individual species and not of a genus-level taxon. However, we believe that the biogeography and fossil record of *Monostiolum* support Dall's separation of it from *Caducifer*.

Pilsbry & Vanatta (1904) subsequently removed *Caducifer* and *Bailya* from the "Aquillidae" (=Cymatiidae, in part) to the Buccinidae on the basis of the radula, but did not mention any species now assigned to *Monostiolum*. Peile (1911), among others, has illustrated the radula of *M. tessellatum*, which proved to be virtually identical with those of *Caducifer* and *Bailya*.

This genus bears a strong resemblance to *Colubraria*, but differs in having only a terminal varix (*Colubraria* has several additional, earlier varices), and in possessing a fully functional radula (*Colubraria* has a vestigial radula). *Colubraria* has been placed by some workers in a family apart from the Buccinidae, the Colubrariidae. However, Beu & Maxwell (1987) have suggested that that group should be included under the buccinid Pisaniinae. They have also shown that several species formerly considered colubrarines are members of the cancellariid subfamily Plesiotritoninae Beu & Maxwell, 1987. *Monostiolum* lacks the noncollabral varix characteristic of that subfamily, although the axial sculpture approaches this condition. Most members of the Plesiotritoninae also possess varices on the spire. The radula of that subfamily is not sufficiently known to warrant comparison with *Monostiolum*.

The species assigned to *Monostiolum* are a heterogeneous group containing some species better belonging to other genera. For example, Kay (1979:261) listed *Caducifer nebulosa* (Gould, 1860) from Hawaii and states that *Caducifer* is "characterized by the tall spire"; this is a reference to *Monostiolum*, not *Caducifer*. "*Caducifer*" *nebulosa* bears little resemblance to any *Monostiolum* and appears to be a member of the columbellid genus *Aesopus* Gould, 1860, the genus in which Gould originally placed it. Several eastern Pacific species that have been placed in *Monostiolum* by Keen (1971) appear to belong to other buccinid genera (such as *Prodotia* Dall, 1924, among others): *biliratum* (Reeve, 1846), *cinis* (Reeve, 1846), *thaleia* Pilsbry & Lowe, 1932, and *nigricostatum* (Reeve, 1846).

Range: Apparently limited to the New World tropics and Bermuda, generally in shallow water under stones and rubble.

Monostiolum tessellatum (Reeve, 1844)

(Figures 1, 2, 6F, 7A, D)

Triton tessellatus Reeve, 1844:pl. 19, fig. 91; Peile, 1911: 227, text fig. (radula).
Caducifer (*Monostiolum*) *tessellatus* (Reeve): Cernohorsky, 1975:196, fig. 50.
Monostiolum tessellatum (Reeve): Beu & Maxwell, 1987: 59.
Pleurotoma igniflua Reeve, 1845:pl. 24, fig. 214.
Pisania (*Monostiolum*) *igniflua* (Reeve): Fulton, 1936:7, 8.
Triton (*Epidromus*) *swifti* Tryon, 1881:31, pl. 16, fig. 158; Fulton, 1936:8.
Colubraria Swiftii [sic] (Tryon): Dall, 1889a:226 [in part]; Dall, 1889b:132.
Colubraria swiftii [sic] (Tryon): Rios, 1975:83, pl. 23, fig. 337.
Colubraria (*Monostiolum*) *swifti* (Tryon): Dall, 1904:136; Abbott, 1954:233; Abbott, 1974:218, fig. 2406.
Monostiolum (*Monostiolum*) *swifti* (Tryon): Ponder, 1972: 255, pl. 24, fig. 7, text fig. 1.8 (radula).
Colubraria swifti (Tryon): Clench [in] Morris, 1973:213, pl. 57, fig. 6; Bandel, 1984:130, fig. 215.
Caducifer (*Monostiolum*) *swifti* (Tryon): Watters, 1983:125, 126, figs. 7–10, 12.
Monostiolum swifti (Tryon): Beu & Maxwell, 1987:59.

Type depositories: *Triton tessellatum* Reeve, 1844—Lectotype, designated herein, BM(NH) 196747/1; 3 paralectotypes, 196747/2-4.

Pleurotoma igniflua Reeve, 1845—BM(NH)?; apparently lost, *fide* Way (*in litt.*, 29 May 1985). Type locality: unknown.

Triton swifti Tryon, 1881—Holotype ANSP 59208. Type locality: Antigua.

Type locality: "Island of Burias, Philippines (found under stones at low water)" (Reeve, 1844:text to species 91); corrected herein to Barbados (see "Remarks").

Description: The maximum size seen is 18 mm in length. The shell is fusiform, the spire being approximately ½ to ⅔ the total length. The protoconch is blunt, consisting of 1½ smooth, rounded whorls. There are approximately 7 postnuclear whorls. The spiral sculpture is of regularly spaced, rounded or flattened cords, often with a smaller thread intercalated between these cords; the cords on the siphonal canal are larger and flattened. The axial sculpture consists of rounded ribs, 15–20 on the penultimate whorl. The spiral cords are often nodulose as they pass over the ribs. The ribs on the body whorl are sigmoidal in shape. In Bermuda, the majority of specimens have weak or absent axial ribs on the body whorl; Antillean specimens, and some Bermudan ones, have persistent ribbing on the body whorl, although it is usually weaker than that on the spire. Numerous microscopic threads are apparent between ribs. Adult shells have a single terminal varix over which all sculpture continues. The inside of the outer lip has approximately 9 weak denticles, the strongest one bounding the anal canal. The parietal callus is adherent to the body whorl for its posterior half and erect and thickened for the remainder of its length. It bears a weak denticle delimiting the siphonal canal and a stronger one bounding the anal canal. The siphonal canal is short, notched, and weakly delimited from the body whorl.

The shell color is very variable, ranging from all white to nearly uniform dark brown. Commonly seen patterns are zig-zag flammulations and checkerboard spots; these two patterns grade into one another in many specimens. A broad, white, spiral band is often vaguely evident below the shoulder of the whorl.

Radula: As for the genus. Illustrated by PEILE (1911) and PONDER (1972) (reproduced here, Figure 7A).

Operculum: Phylliform with a subterminal nucleus (Figure 7D).

Anatomy: Not reported.

Remarks: REEVE (1844) described this species from specimens from the Cuming collection and gave the type locality as the "Island of Burias, Philippines." This locality was in error and there can be little doubt that Reeve's illustration depicts the Caribbean species commonly known as *Colubraria swifti*. The specimen illustrated by Reeve is representative of specimens from the Antillean portion of its range, and an examination of the syntype lot reveals no differences between these specimens and those collected in the Caribbean. TRYON (1881) synonymized *Triton tessellatum* with the Philippine *Triton concinnus* Reeve, 1844, but PEILE (1911) and CERNOHORSKY (1975) have shown that *T. concinnus* is a separate species.

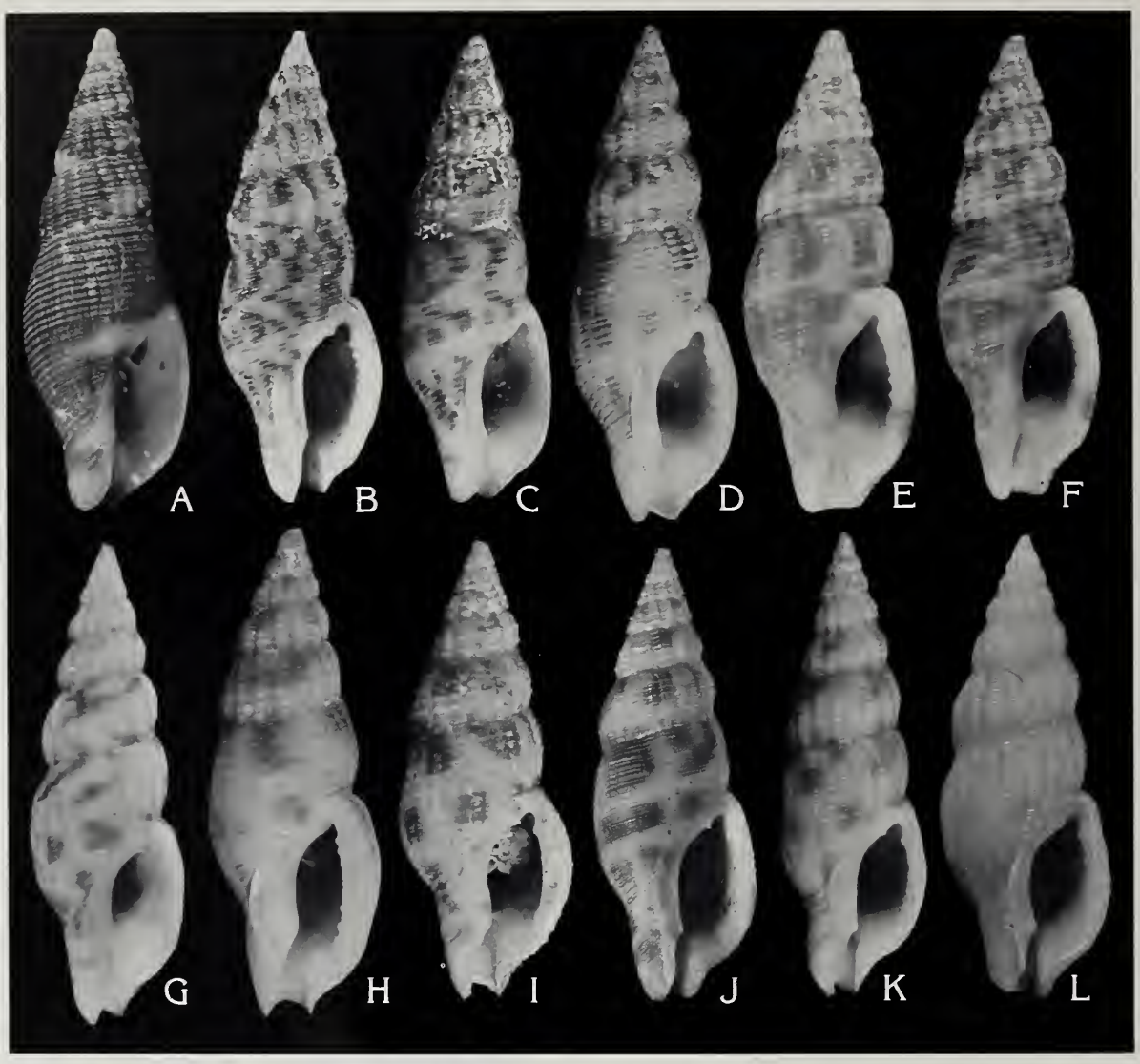
The exact nature of *Triton tessellatum* had been unsuspected for 76 years, when PEILE (1911) suggested that the type locality was incorrect based upon the fact that he had collected the species in Bermuda. He did not however equate it with *T. swifti*. Peile apparently had a highly sculptured, checkerboard-patterned morph which, in the absence of intergrades, does not appear conspecific with the smoother, flammulated morph described as *T. swifti*. CERNOHORSKY (1975) also pointed out that Reeve's original type locality was in error. He suggested that *Monostiolum tessellatum* "very closely resembles . . . *swifti*" (p. 196) and "appears to be a finely sculptured variant of . . . *swifti*" (abstract). Although he did not put *T. swifti* directly in his synonymy of *M. tessellatum*, his abstract statement suggests that he apparently believed them to be the same species.

Both Peile and Cernohorsky suggested that Reeve's original type locality was erroneous, but neither designated a corrected one. For that reason the type locality of *Triton tessellatus* is herein emended to Barbados, where specimens very similar to the syntype lot have been collected.

REEVE (1845) described *Pleurotoma igniflua* from an unknown locality. His illustration clearly shows a specimen of the flammulated morph of *Monostiolum tessellatum*, and Reeve commented that this was a "strongly marked species partaking almost as much of the characters of *Triton* as of *Pleurotoma*" (text to pl. 24). Even given the broad definition of *Pleurotoma* in use at that time, this was an unusual assignment. Not surprisingly, this name escaped notice until FULTON (1936) stated that *P. igniflua* was not a turrid, but should be placed in *Pisania* (*Monostiolum*), and originated from Bermuda. He further suggested that *Pleurotoma igniflua* was "very close to, if not conspecific with, *Triton swifti*" (p. 8). CERNOHORSKY (1975) stated that *T. swifti* was a a junior synonym of *P. igniflua*, and that *P. igniflua* was a junior synonym of *M. tessellatum*. The type (or types) of *P. igniflua*, supposedly in the British Museum (Natural History), are apparently lost (Way, *in litt.*, 29 May 1985), although the illustration leaves no doubt that *P. igniflua* is the common Bermudan morph. FULTON's (1936:8) statement that his specimen of *P. igniflua* "comes from Bermuda" is not considered here to be a subsequent type-locality designation, and in view of the fact that the types are lost, it is prudent not to designate a type locality at this time.

TRYON (1881) described *Triton* (*Epidromus*) *swifti* from Antigua. The holotype is typical of the highly sculptured Antillean morph but is faded. It bears little resemblance to the Bermudan specimens that are now illustrated in field guides and popular works as *Colubraria swifti*. Tryon, in fact, apparently did not recognize the Bermudan morph as *T. swifti*, or even a relative of that species. He assigned *T. tessellatum* to a Philippine species and placed *Pleurotoma igniflua* in the turrid genus *Daphnella*. Thus, the concept of *T. swifti* of later authors and collectors was that of a morph that Tryon did not recognize as his own species.

BEU & MAXWELL (1987) apparently did not recognize *Monostiolum swifti* and *M. tessellatum* as conspecific and made no mention of "*Pleurotoma*" *igniflua*. Their misunderstanding of the variation of this group may have prompted them to suggest that *Bailya* (***Parabailya***) *weberi* was synonymous with *M. tessellatum*.



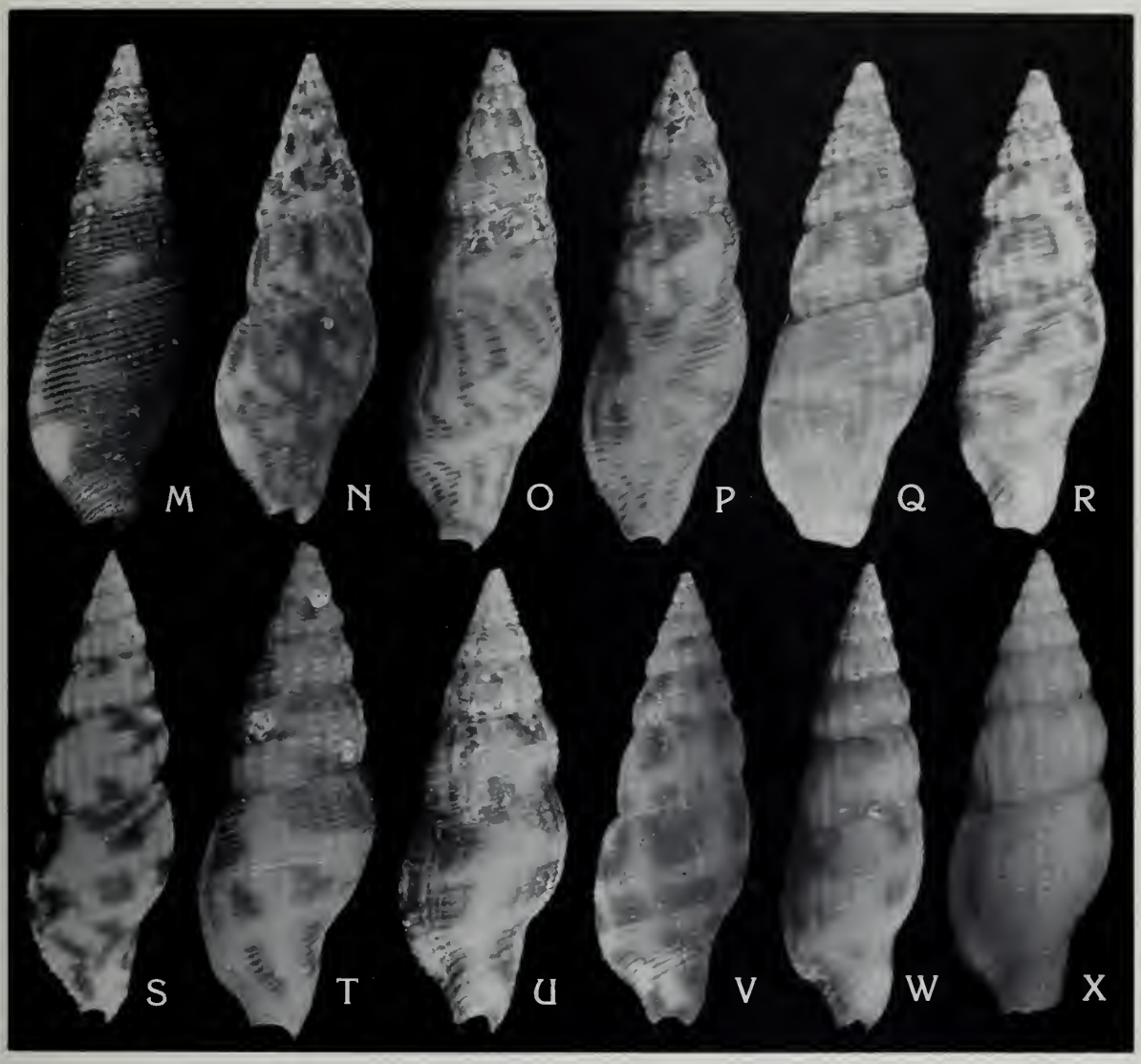
Explanation of Figures 1 and 2

Figures 1 (A–L) and 2 (M–X). *Monostiolum tessellatum* (Reeve, 1844). A, M. DMNH, Coney Island, off Ferry Reach, Bermuda, 16.8 mm. B, N. Bermuda (Watters coll. 4068a), 18 mm. C, O. SW of Whalebone Bay, Bermuda (USNM 835691), 16.9 mm. D, P. Blue Hole, Castle Harbour, Bermuda (USNM 771849), 16.5 mm. E, Q. Grenada

See "Remarks" following the descriptions of *Monostiolum* ***auratum*** sp. nov. and *M.* ***rosewateri*** sp. nov. for comparisons of *M. tessellatum* with those species.

Distribution and habitat: Common in Bermuda, rare throughout the Bahamas, Greater and Lesser Antilles, and off northern Brazil (Figure 8). With the exception of RIOS' (1975) specimen from off San Luiz, Brazil, we can find no records of this species (or any Recent western Atlantic *Monostiolum*) from any continental coast. It is apparently limited to oceanic islands where it occurs in shallow water under rocks and rubble. SANDER & LALLI (1982) reported living specimens of "*swifti*" from 125 and 225 m off Barbados; we have not seen these specimens and they may represent *M.* ***rosewateri***. The present species is most common in Bermuda but occurs sporadically in the Greater and Lesser Antilles. The record from San Luiz is a juvenile specimen from 33 m (Figure 6F) and represents a record far removed from the next nearest locale of Tobago. From this it may be surmised that this species will be found along the intervening Brazilian coast.

Specimens examined: BERMUDA: ANSP 10145, 17822, 36217, 36326, 70156; DMNH 24501; USNM 94410, 149864, 221621, 417730, 663420; Watters coll. 4069a (all "Bermuda"); USNM 656480, NW reefs off Somerset; USNM 658971, SW reef off Somerset; ANSP 319019, Hungry Bay; USNM 714206, Tucker's Town; USNM 771849, Castle Harbour, Blue Hole; USNM 807649, St. George's [Id.]; USNM 621601, W end of St. George's Id.;



(Finlay coll.), 13.2 mm. F, R. Buccoo Reef, Tobago (AMNH 193453), 13.8 mm. G, S. Buccoo Reef, Tobago (AMNH 193322), 17.8 mm. H, T. Bermuda (USNM 221621), 14 mm. I, U. 15–20 fm [27–37 m] off Carlisle Bay, Barbados (USNM 500150), 13.8 mm. J, V. Syntype of *Triton tessellatus* Reeve, 1844, (BM(NH) 1967647), "Isle of Burias, Philippines", 16.6 mm. K, W. 122 fm [22 m] off Carlisle Bay, Barbados (USNM 500149), 17.9 mm. L, X. Holotype of *Triton swifti* Tryon, 1881, (ANSP 59208), Antigua, 16.8 mm.

DMNH 51840, Bailey's Bay; ANSP 145957, Shelly Bay; ANSP 88579, USNM 171930, Gibbet Id.; ANSP 183806, USNM 152157, Hamilton; USNM 835691, SW of Whalebone Bay; DMNH, Coney Island, off Ferry Reach. BAHAMAS: USNM 54542, "Bahamas"; USNM 417731, Bimini. GREATER ANTILLES, CUBA: USNM 678505, Guantanamo Bay. JAMAICA: ANSP 36219, 36220, "Jamaica." DOMINICAN REPUBLIC: USNM 42964, Samaná. LESSER ANTILLES, GRENADA: Finlay coll., "Grenada." BARBADOS: AMNH 193322, "Barbados"; USNM 500148, beach; USNM 500145, Needham Pt.; USNM 500149, 22 m, Carlisle Bay; USNM 500150, 4.6–6 m, Carlisle Bay; USNM 500147, 3–6 m, off Pelican Id.; USNM 459598, off Pelican Id., shallow water. TOBAGO: AMNH 193453, USNM 682304, Buccoo Reef, shallow water; Finlay coll., Arnos Vale beach. BRAZIL: FURG 15.265, Maranhao State, off San Luiz, 33 m.

Monostiolum ***auratum*** Watters & Finlay, sp. nov.

(Figures 3, 7E)

Colubraria swifti: WARMKE & ABBOTT, 1961:117, pl. 21i [*non* Tryon, 1881].

Description: The holotype is 21 mm in length. The shell is fusiform, the spire being approximately ⅔ the total length. The protoconch is blunt, consisting of 1¼ smooth, rounded whorls. The postnuclear whorls are 6¼ to 7½ in number, the first 3 strongly nodulose, subsequent whorls

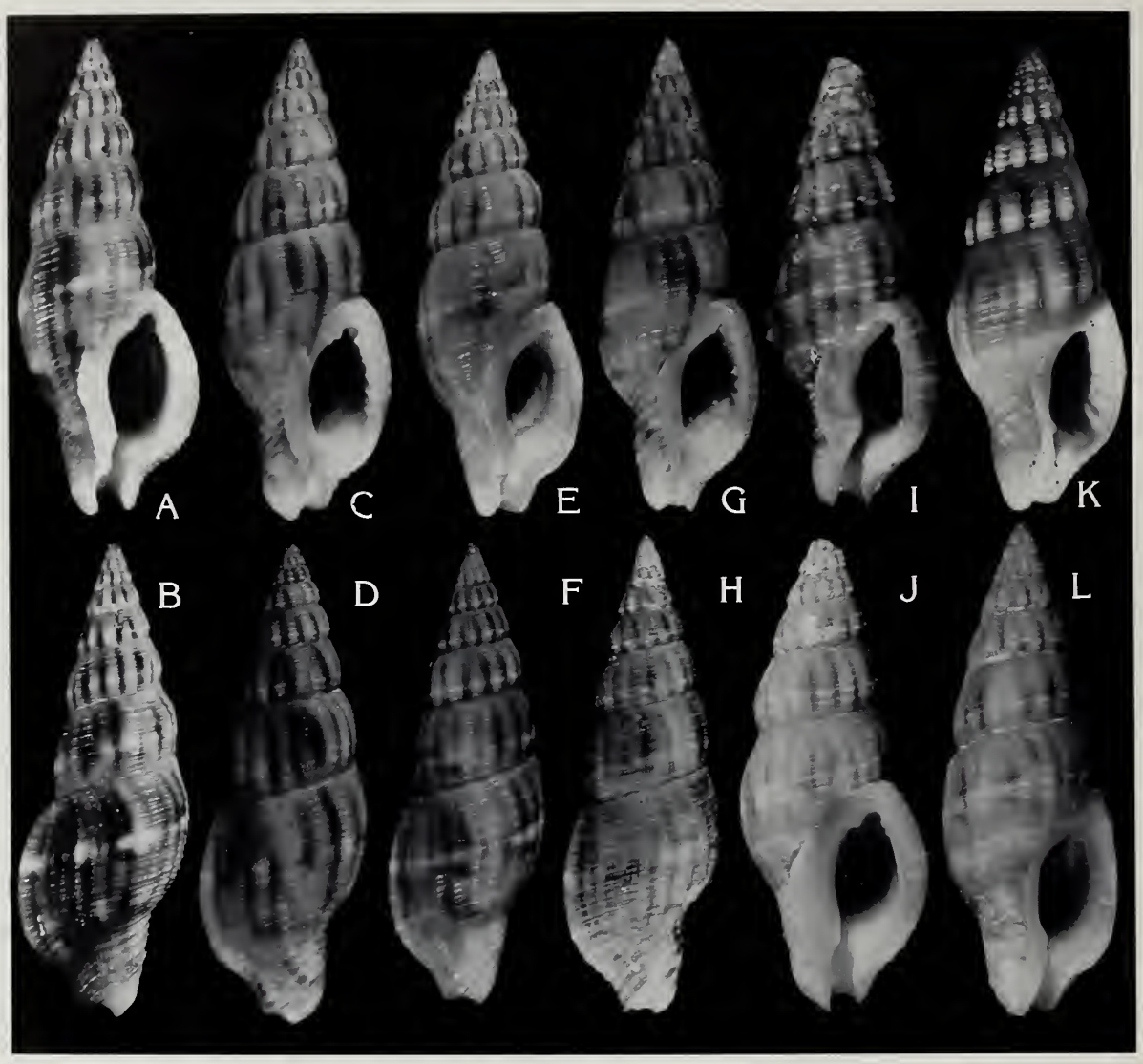


Figure 3

Monostiolum ***auratum*** Watters & Finlay, sp. nov. A, B. Paratype, Rincón, Puerto Rico (BM(NH) 1987065), 18.7 mm. C, D. Paratype, beach at Piñones, 4.8 km E of Boca Cangrejos, Puerto Rico (Finlay coll.), 21.4 mm. E, F. Paratype, Rincón, Puerto Rico (Finlay coll.), 17 mm. G, H. Holotype, Rincón, Puerto Rico (USNM 859960), 21.2 mm. I. N of Pigeon Id. Club, Pigeon Id., St. Lucia (USNM 682388), 14 mm. J. Paratype, Rincón, Puerto Rico (DMNH), 17 mm. K. Paratype, beach at Piñones, 4.8 km E of Boca Cangrejos, Puerto Rico (Finlay coll.), 14 mm. L. Paratype, beach at Piñones, 4.8 km E of Boca Cangrejos, Puerto Rico (DMNH), 16.4 mm.

less so. The spiral sculpture consists of regularly spaced, rounded cords over the entire whorl, which are only slightly stronger on the siphonal canal. Between each cord is a single thread. Axial sculpture consists of rounded ribs, stronger on the earlier whorls, very weak on the body whorl; the penultimate whorl has approximately 18 ribs. Those on the body whorl are sigmoidal in shape and do not persist onto the siphonal canal. Between the spiral cords the surface of the shell is microscopically sculptured with axial threads. Adult specimens have a terminal varix over which all sculpture continues. The inside of the outer lip bears 9–12 irregular denticles just within the lip and several weaker ones deeper within the aperture. The denticles bounding the anal and siphonal canals are strongest. The parietal callus is well developed, adherent to the body whorl along the posterior one-third, erect and thickened anteriorly. Both the anal and siphonal canals are each bounded by a weak denticle. The columella is bent and sharply angled at the posterior canal. The siphonal canal is short and open.

The color of the shell is golden orange with two narrow, interrupted white spiral bands, one at the periphery, one at the base of the body whorl. The spaces between some axial ribs are dark brown, contrasting with the golden ribs. The white spiral bands do not cross these brown axial regions. The aperture is white. Living specimens and fresh shells are a dark grayish green, referring perhaps to a periostracum. No specimens that we have seen have retained that color.

Radula, operculum, and anatomy unknown.

Type depositories: Holotype: USNM 859960.

Paratypes: BM(NH) 1987065, Rincón, Puerto Rico (one specimen); DMNH, Rincón, Puerto Rico (1 specimen); DMNH, beach at Piñones, 4.8 km E of Boca de Cangrejos, Puerto Rico (1 specimen); Finlay coll., Rincón, Puerto Rico (1 specimen); Finlay coll., beach at Piñones, 4.8 km E of Boca de Cangrejos, Puerto Rico (2 specimens); Finlay coll., 9–12 m, Tortuguero Bay [Puerto del Tortuguero], Puerto Rico (1 specimen).

Type locality: Rincón, Puerto Rico, in beach drift, 17°57′N, 66°20′W, H. H. Monroe, 1949 (*ex* J. Finlay coll.)

Other material examined: Lesser Antilles, Puerto Rico: ANSP 228472 "Puerto Rico"; USNM 598298, 24 km E of "Beringuen" [Punta Borinquen]. St. Lucia: USNM 682388, Pigeon Id., N of Pigeon Id. Club. Barbados: USNM 19534, "Barbados."

Etymology: Latin *auratum,* meaning "golden" or "gilded," in reference to the color of the shell.

Distribution and habitat: This striking species is infrequently found in beach drift in Puerto Rico and is very rare throughout the Lesser Antilles (Figure 8). It has been collected alive only once to my knowledge—from perhaps 9–12 m, off Tortuguero Bay, Puerto Rico, but the depth is not precisely known. Presumably living under rubble.

Remarks: The specimen of "*swifti*" illustrated by Warmke & Abbott (1961:pl. 21i) is this species. The "*swifti*" of Arnow *et al.* (1963), Mestey-Villamil (1980), and Ortiz-Corps (1983) may also refer to *Monostiolum* ***auratum*** but the specimens are not illustrated or are mentioned only in checklists. The only non-Puerto Rican specimens that we have seen are more coarsely sculptured, less fusiform, and darker in color with the brown spaces between the ribs less pronounced. Too few examples are at hand to suggest a clinal variation.

This species tends to be more slender and have a higher spire than either *Monostiolum tessellatum* or *M.* ***rosewateri*** sp. nov. The axial ribs of *M.* ***auratum*** persist onto the last ¼ of the body whorl but are usually absent or weak in *M. tessellatum. Monostiolum* ***auratum*** never has the flammulated or tessellated color pattern of *M. tessellatum.* The striking golden color of the shell, with dark brown interstices between the axial ribs, does not occur in any other species of *Monostiolum.*

Monostiolum ***rosewateri*** Watters & Finlay, sp. nov.

(Figure 4)

Colubraria Swiftii: Dall, 1889b:226 [in part].
Colubraria (*Monostiolum*) sp.: Sander & Lalli, 1982:316.

Description: The holotype is 15.7 mm in length. The shell is fusiform, the spire being slightly longer than ½ the total length. The protoconch is blunt, consisting of 1½ smooth, rounded whorls. There are 6–7¼ postnuclear whorls. The spiral sculpture consists of regularly spaced cords with a spiral thread intercalated between them, the sculpture stronger on the axial ribs. The axial sculpture consists of rounded ribs, which are prominent on the earlier whorls, but more subdued on the body whorl. The penultimate whorl has 10–12 axial ribs. Adult specimens have a prominent, heavy terminal varix over which sculpture continues. The inside of the outer lip has 7–9 lirate teeth; the teeth bounding the canals are strongest. The parietal wall is adherent to the body whorl for most of its length. The anal and siphonal canals are bounded on the columella by weak denticles. The columella is bent but not strongly so. The siphonal canal is short, open, and notched.

The color of the shell is cream to yellowish tan with irregular whitish blotches. Two vague white spiral bands may be evident at the periphery and at the base of the body whorl. The holotype has most of the major spiral cords colored brown as they pass over the axial ribs. Paratype AMNH 112353 has less defined brown cords, and additional paratypes show no evidence of this coloration. Aperture white.

Radula, operculum, and anatomy unknown.

Type depositories: Holotype: USNM 87098.

Paratypes: AMNH 112353, W side Barbados (2 specimens); Redpath Museum 16301, *Diadema* Sta. 55, 125 fm [229 m], off St. James and Speightstown, W Barbados, on sand bottom (1 specimen).

Type locality: W Barbados, *Blake* Sta. 272, 76 fm [139 m, approximately 13°10′N, 59°40′W].

Other material examined: *Diadema* Sta. 69, 100 fm [186 m], off Coral Beach, W Barbados, on sand and shell bottom (Redpath Museum [not catalogued]).

Etymology: This species is named after the late Dr. Joseph Rosewater of USNM, in recognition of his many malacological achievements and his enthusiasm and constant willingness to aid amateurs and professionals alike.

Distribution and habitat: The meager evidence available indicates that this species is endemic to offshore Barbados (Figure 8). Specimens have been found from 139 to 229 m depth. Sander & Lalli (1982) listed shells of an unidentified species of *Monostiolum* from 125 and 175 m, off Barbados. Dr. Sander was kind enough to forward the specimen taken at 175 m to us for examination, but the specimen was crushed *en route* through the Postal Service.

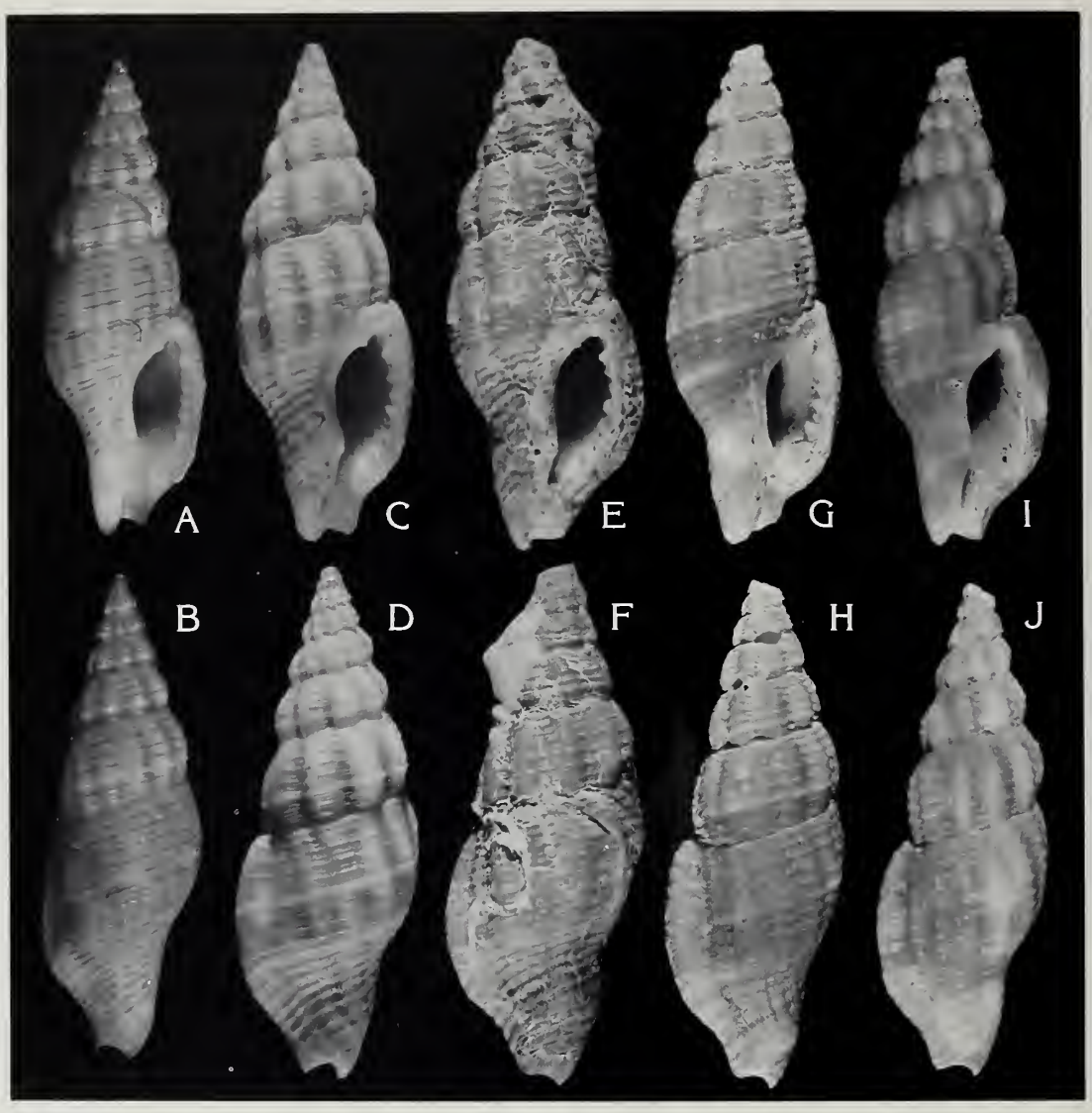


Figure 4

Monostiolum ***rosewateri*** Watters & Finlay, sp. nov. A, B. Holotype, *Blake* Sta. 272, 76 fm [139 m], Barbados (USNM 87098), 15.9 mm. C, D. Paratype, *Diadema* Sta. 55, 125 fm [227 m], off St. James and Speighstown, W Barbados (Redpath Museum 16301), 14.4 mm. E, F. *Diadema* Sta. 69, 100 fm [183 m], off Coral Beach, W Barbados (Redpath Museum, not catalogued), 15 mm., G, H. Paratype, W Barbados (AMNH 112353), 19 mm. I, J. Paratype, W Barbados (AMNH 112353), 18 mm.

The fragments indicate that this was a specimen of *M.* ***rosewateri***. We have not seen the specimen collected from 125 m. The habitat is unknown but it has been found on shell-sand substrates. However, these specimens were inhabited by hermit crabs.

Remarks: It does not seem to be closely related to any other member of the genus but its affinities may be to *Monostiolum tessellatum*. This species differs from *M. tessellatum* in its having fewer, more prominent, axial ribs (15–20 on the penultimate whorl of *M. tessellatum,* 10–12 on *M.* ***rosewateri***). These ribs persist onto the last ¼ of the body whorl in *M.* ***rosewateri*** but are usually absent or weak on this area in *M. tessellatum*. None of the known specimens of *M.* ***rosewateri*** has the flammulated or tessellated color pattern of *M. tessellatum*. *Monostiolum* ***auratum*** also has more axial ribs (ca. 18) on the penultimate whorl and a typically higher spire than does *M.* ***rosewateri***. *Monostiolum* ***rosewateri*** also lacks the gold and brown color pattern of *M.* ***auratum***. The parietal shield is more

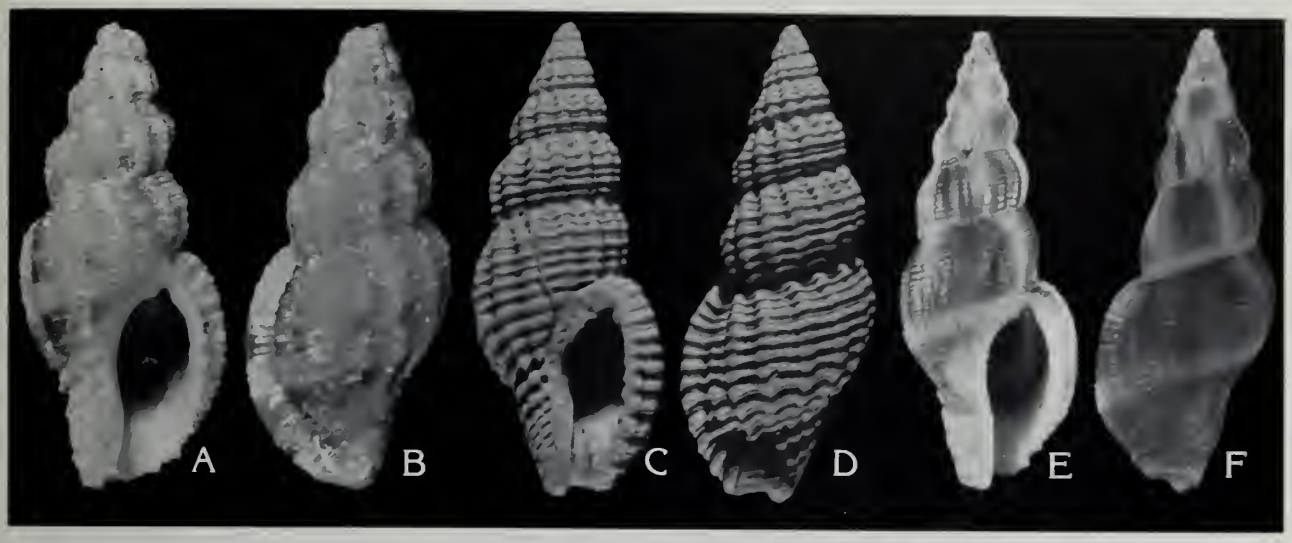


Figure 5

Representative *Bailya* and ***Parabailya*** Watters & Finlay, subgen. nov. A, B. *Bailya parva* (C. B. Adams, 1850), 0.5 mi N of Governor's house, 7 Mile Beach, Grand Cayman Id. (DMNH 39582), 16 mm. C, D. *Bailya roycei* (M. Smith, 1938), St. Petersburg, Florida (ANSP 19064), 13.4 mm. E, F. *Bailya* (***Parabailya***) *weberi* (Watters, 1983), holotype of *Caducifer* (*Monostiolum*) *weberi* Watters, 1983, 73 m, off Looe Key, Monroe Co., Florida (ANSP 355365), 16 mm.

adherent to the columella in *M.* ***rosewateri*** than in the other two species.

Bailya M. Smith, 1944

Parabailya Watters & Finlay, subgen. nov.

(Figures 5E, F)

Type species: *Caducifer* (*Monostiolum*) *weberi* Watters, 1983 (Figures 5E, F).

Description: The shell is small (10–20 mm in length), fusiform, the spire comprising approximately ⅗ the total length. The protoconch is blunt, consisting of 1½ smooth, rounded whorls. The postnuclear whorls are approximately 7 in number, abruptly arising from the protoconch, the earlier postnuclear whorls being strongly sculptured, becoming less so on successive whorls. The postnuclear sculpture consists of distinct spiral threads separated by grooves of equal width. The axial ribs become less pronounced and more irregularly spaced on later whorls, becoming barely perceptible on the last ½ whorl. The threads do not diminish in strength as they pass over the axial ribs. Several threads on the siphonal canal are distinctly wider and more pronounced than those of the remaining portion of the whorl. The last ¼ whorl flares outward to form a terminal varix. The aperture is oval, weakly crenulated, the anal canal being bounded by a tooth on the outer lip and another on the body whorl. The columella is straight, the inner lip is adherent, terminating in a short, open, siphonal canal; the siphonal canal notch is shallow.

Radula, operculum, and anatomy unknown.

Etymology: *para*, meaning "beside" or "akin to," and *Bailya*, a genus of tropical, New World buccinids erected by Maxwell Smith in 1944, the type of which is *B. anomala* (Hinds, 1844) from the eastern Pacific.

Remarks: The only known species of ***Parabailya*** at this time is *Bailya weberi* (Watters, 1983), which the senior author originally placed in *Caducifer* (*Monostiolum*). Since that time the differences between *B. weberi* and other species of *Monostiolum*, and the unnoticed resemblances to *Bailya*, have convinced us of the need for a new subgenus-level taxon for that species. All of the four known species of *Bailya s.s.* have coarse axial and spiral sculpture, and a spire that occupies one-half or less of the total length of the shell. Conversely, *B. weberi* has relatively smooth sculpture and a proportionally higher spire, as do most Recent species of *Monostiolum*. Because of the overall shape of the shell and its sculpture, *B. weberi* closely resembles *Monostiolum*. However, all known members of *Monostiolum* have a columella that is distinctly angled at the point of the juncture of the siphonal canal and the body whorl, and the inner lip is typically only partially adherent along its length. In *Bailya s.s.* and ***Parabailya*** the columella is not angled and is adherent its entire length. Reconsideration of the apertural features and fossil species suggest that *B.*

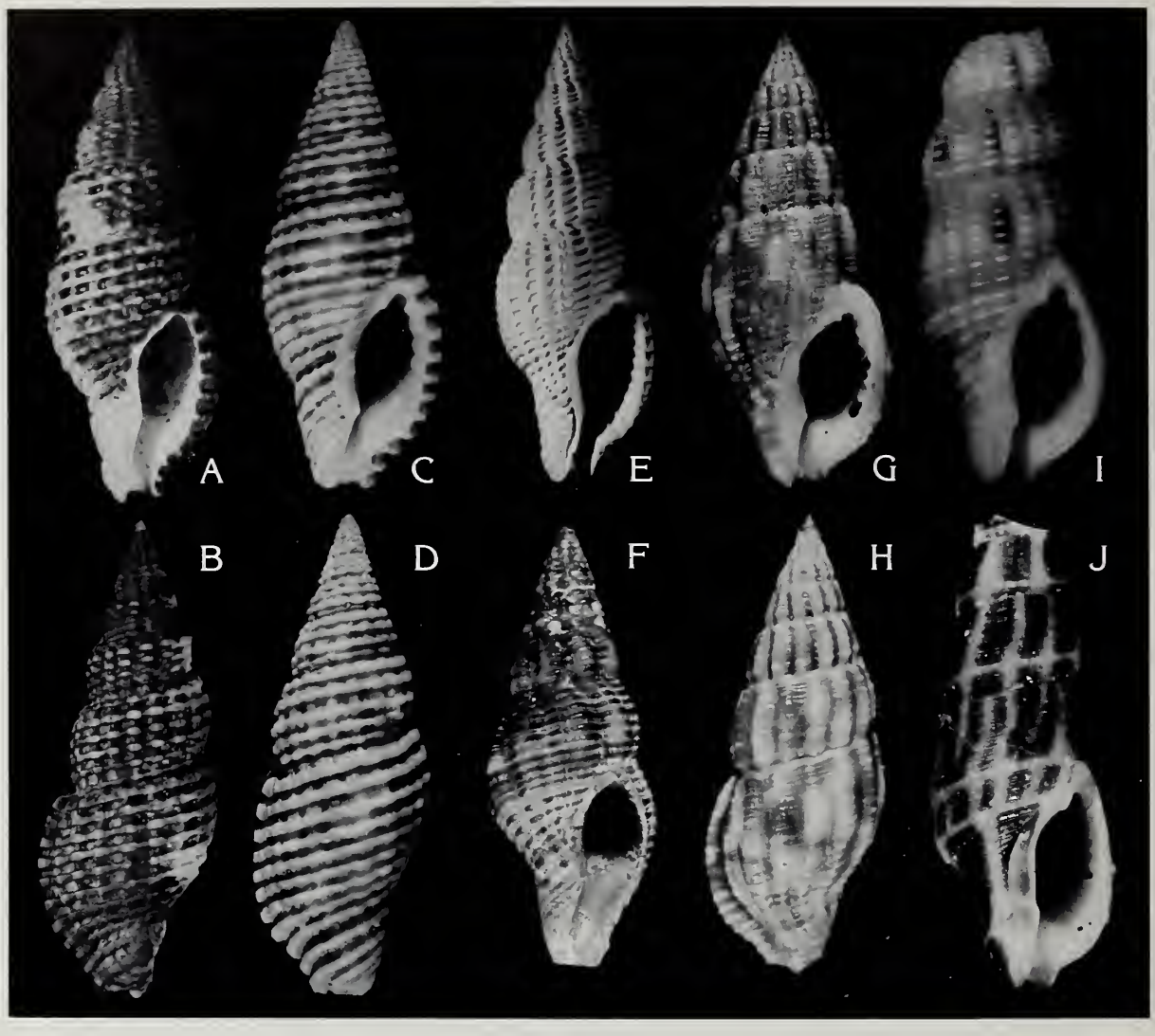


Figure 6

Representatives of *Monostiolum* and *Caducifer*. A, B. *Monostiolum petiti* Olsson, 1967, holotype, Pliocene, Waccamaw beds at Crescent Beach Airport, Horry Co., South Carolina (USNM 645173), 16.4 mm. C, D. *Monostiolum crebristriatum* (Carpenter, 1856), holotype of *Triton crebristriatus* Carpenter, 1856, Panama Bay (BM(NH) 19621120), 17.5 mm. E. *Monostiolum thomasi* Olsson, 1967, holotype, Pliocene, Caloosahatchee River Formation, Unit A, west of Ortona Locks, Glades Co., Florida (USNM 645172), 21 mm. F. *Monostiolum tessellatum* (Reeve, 1844), 33 m, off San Luiz, Maranhao State, Brazil (FURG 15.265), 11.5 mm. G, H. *Monostiolum pictum* (Reeve, 1844), syntype of *Triton pictus* Reeve, 1844, Galápagos Islands BM(NH), 16.4 mm. I. *Caducifer* sp., reef between Turuaimu and Rikumanu, Kapinga [?=Kaiping, Liaoning Prov.], China (USNM 622377), 18 mm. J. *Caducifer decapitatus* (Reeve, 1844), Ine, Arno Id., Ratak Chain, Marshall Ids. (USNM 634985), 13.5 mm.

weberi is more similar to *Bailya* and represents a new subgenus exhibiting some *Monostiolum* characteristics.

Beu & Maxwell (1987:59) incorrectly stated that *Bailya* (***Parabailya***) *weberi* "is almost certainly *M. tessellatum*." However, they were unaware of the true nature of *Monostiolum* in the western Atlantic and did not see the connection between that genus and *Bailya*.

DISCUSSION

Paleontological Record of *Monostiolum* and *Bailya*

Dall & Ochsner (1928) described a species of *Monostiolum* as *Colubraria pervaricosa* from the Pleistocene of Vilamil, Albemarle Island [Isla Isabela], Galápagos Islands. They stated (p. 108): "This species is not distantly

related to the forms found in the Antilles, as well as many of other parts of the world." It appears to be closely related to *M. **auratum*** and the Recent Galápagos species *M. pictum* (Reeve, 1844) (Figures 6G, H) in overall form and sculpture. KEEN (1971) has suggested that *M. pervaricosum* is synonymous with *M. pictum,* but we prefer to leave *M. pervaricosum* as a distinct species until more material can be studied.

OLSSON (1967) described two fossil *Monostiolum* from the western Atlantic: *M. thomasi* (Figure 6E) from the Caloosahatchee River formation, Unit A, west of Ortona Locks, Glades County, Florida; and *M. petiti* (Figures 6A, B) from the Waccamaw beds at Crescent Beach Airport, Horry County, South Carolina. Both are believed to be Pliocene in age. The stated differences between the two species are well within the range of variation of any single species of *Monostiolum,* but without more material at hand it would be premature to synonymize them. These taxa bear a striking resemblance to the Recent tropical western American species *Monostiolum crebristriatum* (Carpenter, 1856) (of which *M. tabogensis* Pilsbry & Lowe, 1932, is a synonym) (Figures 6C, D); the latter may represent a descendant of that line.

The species *Phos roycei* M. Smith, 1938 (Figures 5C, D), later placed by M. SMITH (1944) in his genus *Bailya,* was described from the Pliocene of Clewiston, Hendry County, Florida. OLSSON & HARBISON (1953) illustrated a specimen of this species from the Pliocene of St. Petersburg, Florida, remarking (p. 260): "this species is near [*Bailya intricata* (Dall, 1884), specimens of which at ANSP] are more heavily shouldered and the spiral sculpture is sharper than in the fossil species." The spiral sculpture is indeed sharper in the Recent species but not as strong as that in *B. roycei.*

Phylogeny of *Monostiolum, Bailya,* and ***Parabailya***

Comparison of Recent members of *Caducifer* (Figures 6I, J) with *Monostiolum,* based upon conchological evidence, suggests that the two are closely related. With the exception of a decollated spire, shell characteristics are virtually inseparable between *Caducifer* and western Atlantic species of *Monostiolum.* (As previously mentioned, many of the species assigned to *Monostiolum* do not appear to belong there. The eastern Pacific species in particular represent a polyphyletic group of which few species will probably be found to be in *Monostiolum.* There is also some confusion in the literature concerning the taxonomy of species of *Caducifer*: the names *truncata* Hinds; 1844, *decapitatus* Reeve, 1844; *cylindrica* Pease, 1868; and *decollata* Sowerby I, 1833, have not been uniformly applied to these taxa; while all of these names appear to be referable to *Caducifer,* the status of the nominal species has yet to be adequately documented.) Juvenile specimens of *Caducifer* have a protoconch virtually identical to those of *Monostiolum* and *Bailya* (Figures 7E–G). PILSBRY & VANATTA (1904) and PONDER (1972) have illustrated the radulae of *Caducifer, Bailya,* and *Monostiolum*; we can find no pertinent differences among them (Figures 7A–C).

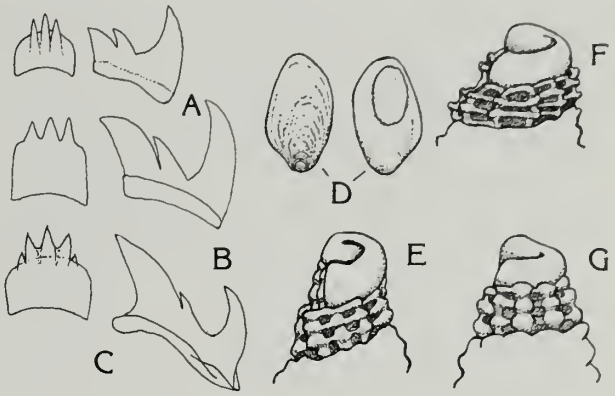


Figure 7

Radulae, operculum, and nuclear whorls. A. Partial radular row of *Monostiolum tessellatum* (Reeve, 1844), redrawn from PONDER (1972:fig. 1.8). B. Partial radular row of *Bailya parva* (C. B. Adams, 1850), redrawn from PILSBRY & VANATTA (1904:fig. 5). C. Partial radular row of *Caducifer decollata* (Sowerby I, 1833), redrawn from PONDER (1972:fig. 1.3). D. Operculum of *Monostiolum tessellatum* (Reeve, 1844), Bermuda (USNM 663420). E. Nuclear whorls of *Monostiolum **auratum*** Watters & Finlay, sp. nov., Rincón, Puerto Rico, holotype (USNM 859960). F. Nuclear whorls of *Bailya intricata* (Dall, 1884), Sambo Reef, Florida (Watters coll. 5536a). G. Nuclear whorls of *Caducifer* sp., Easter Id. (USNM 638945).

The species of *Monostiolum* are restricted to the New World tropics. *Caducifer* is found in the Indo-Pacific tropics, and a species has been found off Brazil: *Caducifer atlantica* Coelho, Matthews & Cardoso, 1970. *Monstiolum* appeared in the western arm of the Tethys Sea in the New World prior to the Pliocene closing of the Isthmus of Panama. A fossil representative of this group is *M. pervaricosum,* and Recent species are *M. tessellatum, M. **auratum**, M. pictum,* and perhaps *M. **rosewateri**.* All Recent species are associated with oceanic islands, rarely on continental margins. The widespread Recent *M. tessellatum* has no known living or fossil relatives with the possible exception of *M. **rosewateri**.* The Recent Caribbean *M. **auratum*** is conchologically similar to the Recent eastern Pacific *M. pictum* and the fossil *M. pervaricosum*; the fossil Caribbean *M. petiti* and *M. thomasi* are very similar to the Recent eastern Pacific *M. crebristriatum.*

The earliest known *Bailya, B. roycei* from the Florida Pliocene, differs from *Monostiolum* primarily in the features of the columella and the relatively strong sculpture. *Bailya* (***Parabailya***) *weberi,* which possesses several *Monostiolum*-like features, is a smooth-sculptured, high-spired species that is otherwise similar to *Bailya.*

Both *Bailya* and *Monostiolum* have produced lines of

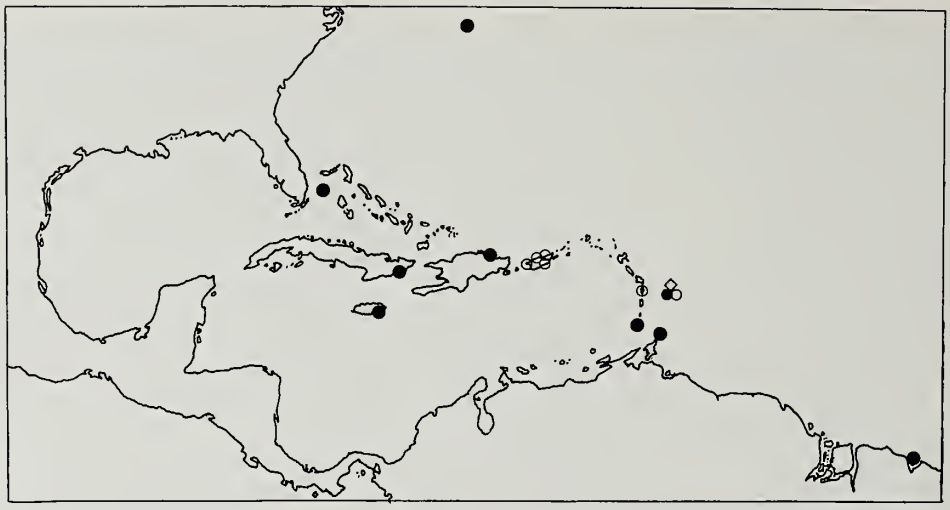


Figure 8

Distribution of western Atlantic *Monostiolum*. Solid circles represent *M. tessellatum* (Reeve, 1844); open circles represent *M. **auratum*** Watters & Finlay, sp. nov.; diamond represents *M. **rosewateri*** Watters & Finlay, sp. nov.

heavily sculptured species. *Bailya* species include *B. anomala* in the tropical eastern Pacific, and *B. parva* (C. B. Adams, 1852) (Figures 5A, B), *B. intricata* (Dall, 1884), and *B. roycei* in the western Atlantic. *Monostiolum* includes such heavily sculptured species as *M. petiti* and *M. thomasi* in the western Atlantic and *M. crebristriatum* in the eastern Pacific. No known living descendants of the heavily sculptured *Monostiolum* line exist in the western Atlantic. Both *Bailya* and *Monostiolum* probably produced these lineages prior to the closing of the Isthmus of Panama. These ribbed forms may have evolved in the Cenozoic as part of a general trend in gastropods to develop heavily sculptured, predation-resistant shells (VERMEIJ *et al.*, 1981; VERMEIJ, 1983a). However, most species of *Monostiolum* (as well as of ***Parabailya*** and *Caducifer*) have evolved smoother shells possibly constructed to withstand peeling of the aperture by predators such as calappid crabs (VERMEIJ, 1982, 1983b). These shells have such features as a narrow aperture bounded by a thick varix and a high-spired shell. It is likely that the relatively smooth sculpture may also make the shell difficult to hold by the predator.

Zoogeography of *Monostiolum*

The zoogeography of the living species of *Monostiolum* appears to be related to plate tectonics in the Cenozoic (see ROSEN, 1985, for a review of Caribbean tectonic models) or habitat differences associated with these plates. The distribution of *M. **auratum*** is associated with the Caribbean plate where it occurs on the leading edge of the plate at what is now Puerto Rico and the Lesser Antilles. It has been found only on oceanic islands; the similar *M. pervaricosum* and *M. pictum* are also only associated with offshore islands, the Galápagos Islands.

Monostiolum tessellatum is associated with the islands of the North American plate. Both *M. **auratum*** and *M. tessellatum* occur along islands at the subduction zone where the two plates meet and there has been little dispersal across them. This separation may be due in part to the fact that *Monostiolum* has a paucispiral protoconch, which is indicative of a short-term larval dispersal stage and (or) direct development within the egg case to a juvenile, without a free-swimming stage.

*Monostiolum **rosewateri*** is known only from deep water off Barbados and does not appear to be closely related to any other species. It is likely a descendant of the shallow-water *M. tessellatum*, which also occurs there.

The heavily sculptured species *Monostiolum crebristriatum, M. petiti,* and *M. thomasi* are all conchologically similar and associated with the North American continent rather than offshore islands. The ancestors of this group were probably distributed along the southern margin of the continent and were subsequently separated by the emergence of Central America. The eastern populations became extinct, leaving only the Recent *M. crebristriatum* in the eastern Pacific.

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Description of Two New Species of the Genus *Chicoreus* (Gastropoda: Muricidae) from Southern Africa

by

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Abstract. Two new species—*Chicoreus* ***fosterorum*** and *C.* ***zululandensis***—are described from southern Africa and compared with *Chicoreus cloveri* Houart, 1985, *C. crosnieri* Houart, 1985, *C. nobilis* Shikama, 1977, *C. rossiteri* (Crosse, 1872), and *C. ryukyuensis* Shikama, 1978. Protoconchs are illustrated for comparison.

INTRODUCTION

In the course of the revision of the genus *Chicoreus* from the Indo-West Pacific (Houart, in preparation), all species, fossil and Recent, were carefully studied and type material, as well as a great number of specimens, examined. The result of this investigation was the discovery of several new species of which a majority already have been named in previous papers (Houart, 1983, 1984, 1985; Houart & Pain, 1982). The present paper describes two new South African species now included in what I call the *Chicoreus aculeatus* group (*C. aculeatus* (Lamarck, 1822) being the oldest taxon of this group).

SYSTEMATIC DESCRIPTIONS

Family Muricidae Rafinesque, 1815

Subfamily Muricinae Rafinesque, 1815

Genus *Chicoreus* Montfort, 1810

Chicoreus ***fosterorum*** Houart, sp. nov.

(Figures 1–5)

Type material: Holotype NM 5343 (36.5 mm); 1 paratype NM E2031 (51 mm); 1 paratype R. Houart collection (41 mm) (*ex* Glass and Foster); 1 paratype No. 86-083, Glass and Foster collection (46.5 mm).

Type locality: Mzamba, Pondoland, Transkei, South Africa, ca. 30°51′S, 29°46′E; no other data known.

Paratypes: NM E2031: East Transkei, between Mtentu and Mzamba rivers, between about 30°51′S, 29°46′E and 31°33′S, 28°31′E; Glass and Foster and Houart collections: on Aliwal Shoal, south coast of Natal, 30°15′S, 30°49′E, 50 m depth.

Description: Shell small and solid, up to 51 mm in length. Spire high, consisting of 2 protoconch whorls and 5 teleoconch whorls. Protoconch large and globose. Suture appressed. Last whorl bearing 3 frondose varices ornamented with 5 short and foliaceous spines. Shoulder spine broad and very frondose, other spines short and broadly open; anterior spine largest, with short intermediate spinelets. Intervarical axial sculpture consisting of a single, prominent node. Spiral sculpture consisting of numerous squamous cords and threads on the whole surface. Aperture roundly ovate. Columellar lip adherent to the shell and slightly erect anteriorly, smooth. Anal notch narrow and

→

Explanation of Figures 1 to 8

Figures 1–5. *Chicoreus* ***fosterorum*** sp. nov. 1 and 2: holotype NM 5342, 36.5 × 17.5 mm. 3: paratype R. Houart collection, 41 × 22.5 mm. 4: paratype Glass and Foster collection No. 86-083, 46.5 × 25 mm. 5: protoconch (paratype Glass and Foster collection). Scale: 0.5 mm.

Figures 6–8. *Chicoreus* ***zululandensis*** sp. nov. 6 and 7: holotype NM D8049, 31.5 × 16.2 mm. 8: protoconch (holotype). Scale: 0.5 mm.

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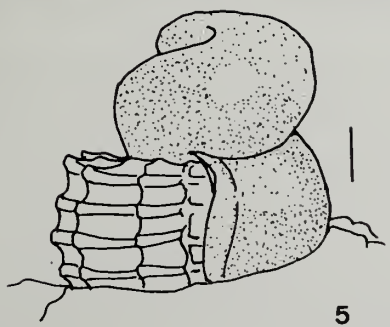
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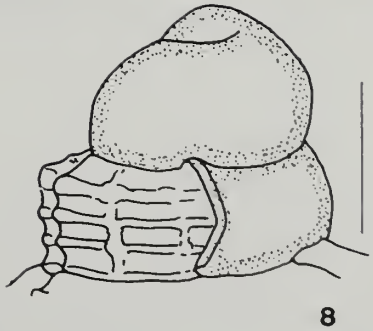
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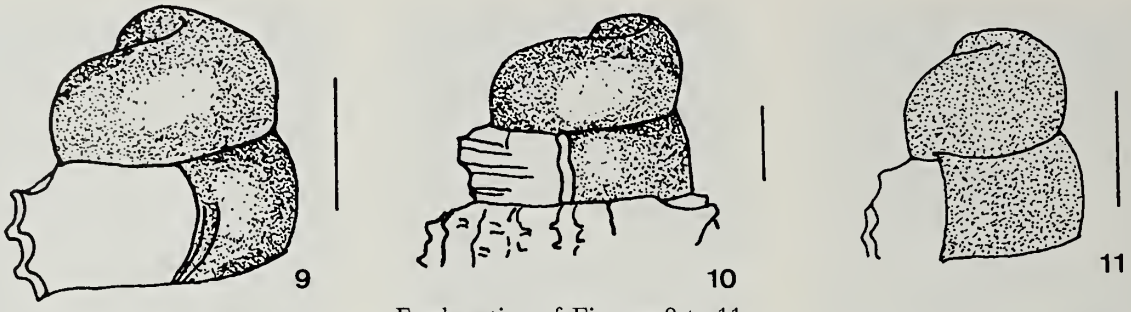

Explanation of Figures 9 to 11

Figure 9. Protoconch of *Chicoreus cloveri* Houart, 1985 (paratype R. Houart collection).

Figure 10. Protoconch of *Chicoreus crosnieri* Houart, 1985 (holotype MNHN).

Figure 11. Protoconch of *Chicoreus ryukyuensis* Shikama, 1978 (Kanagawa Prefectural Museum, No. 3281).

fairly deep. Outer apertural lip crenulate, briefly striate inside. Siphonal canal long, narrowly open and slightly bent backwards at the tip. Ornamented by 3 or 4 short, straight, frondose and broadly open spines. Color white, with protoconch and first 3 or 4 spire whorls pinkish orange.

Discussion: Included in a small group of species from the Indo-West Pacific region, *Chicoreus* ***fosterorum*** is morphologically most similar to three of those species, namely *C. cloveri* Houart, 1985, *C. nobilis* Shikama, 1977, and *C. ryukyuensis* Shikama, 1978. *Chicoreus cloveri* is smaller with a much smaller protoconch (Figure 9), less frondose spines with different ornamentation on the siphonal canal, the spines being smaller and situated anteriorly on the canal. The anal notch of *C. cloveri* is larger and the anterior end of its columellar lip is recurved and thickened, but straight and smooth for *C.* ***fosterorum***. From *C. nobilis* the new species differs by its paucispiral and globose protoconch, which is conical and multispiral in *C. nobilis,* which also has a broader anal notch, 2 or 3 intervarical axial ridges and a different ornamentation of the varices and siphonal canal, consisting of fewer and longer spines. *Chicoreus ryukyuensis* is similar, although having less frondose spines, a comparatively smaller protoconch with different terminal varix (Figure 11), a broader and larger anal notch, and more ovate aperture.

Etymology: Named for Robert Foster and his daughters, of Santa Barbara, California, whose loans and donation of one paratype are appreciated.

Chicoreus ***zululandensis*** Houart, sp. nov.

(Figures 6–8)

Type material: Holotype NM D8049 (31.5 mm); 1 paratype NM D6733 (34.5 mm); 1 paratype R. Houart collection (30 mm) (*ex* NM D8051).

Type locality: North Zululand: SE of Kosi River mouth, 26°55.0′S, 32°55.8′E, 65 m depth, sponge, gorgonians, medium sand. Dredged by RV *Meiring Naudé,* 7 June 1987.

Paratypes: North Zululand, off Jesser Point, 27°32.8′S, 32°42.6′E, 68 m, sponge, coral rubble. Dredged by RV *Meiring Naudé,* 3 June 1987.

Description: Shell small, length up to 34.5 mm. Spire high, consisting of 2 protoconch whorls and 6 to 7 rounded teleoconch whorls. Protoconch rounded and smooth. Suture appressed. Last whorl bearing 3 frondose varices ornamented with 4 moderately sized, slightly foliaceous and upward curved, open spines. Shoulder spine shortest, sometimes obsolete; anterior spine longest. Intervarical axial sculpture consisting of 1 or 2 strong nodes. Spiral sculpture of numerous crowded squamous cords and threads. Aperture rounded. Columellar lip smooth, briefly and partially erect anteriorly. Anal notch deep and narrow, relatively small. Outer apertural lip slightly erect, crenulate, briefly and shallowly striate inside. Siphonal canal long, narrowly open, straight and very slightly bent backwards on the tip; bearing 2 equal-sized open and foliaceous spines. Color pinkish orange with paler shades, especially on the varices.

Discussion: This new species is undoubtedly related to *Chicoreus rossiteri* and *C. crosnieri.* It differs from the first in its very different protoconch, *C. rossiteri* having planktotrophic larval development with a multispiral and conical protoconch, while the paucispiral protoconch whorls of the new species indicate lecithotrophic development. The primary spiral cords are more numerous for *C.* ***zululandensis*** and both spiral cords and threads are finer. From *C. crosnieri* it differs also in its different protoconch, that of *C. crosnieri* being flatter with a different terminal varix (Figure 10). The spiral cords of the new species are narrower and more numerous, and the ornamentation of the siphonal canal is different, the spines of *C. crosnieri* being strongly bent downwards.

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Opisthobranch Range Extensions in Alaska with the First Records of *Cuthona viridis* (Forbes, 1840) from the Pacific

by

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Abstract. The known ranges of 15 species of opisthobranch mollusks are extended northward to the vicinity of Ketchikan, Alaska. The presence of *Cuthona viridis* (Forbes, 1840) is recorded from the Pacific for the first time and an expanded species description is given.

The known ranges of opisthobranch mollusks occurring in Alaska have recently been summarized by LEE & FOSTER (1985). Since then, two additional species have been added, *Doridella steinbergae* (Lance, 1962) and *Hermaea vancouverensis* O'Donoghue, 1924 (FOSTER, 1987a, b). In June 1987, Sven Donaldson and I made a trip to Ketchikan, Alaska (55°25'N, 131°40'W). With the help of local divers, 10 dives were made, at six sites, all in the vicinity of Ketchikan (Figure 1). A total of 43 species of opisthobranchs were collected. The known ranges of 15 of these species are extended northward in this paper. The first Pacific records for *Cuthona viridis* (Forbes, 1840) are given, together with an expanded species description.

DESCRIPTION OF *Cuthona viridis*

Material: 3 June 1987, one specimen 8 mm long, 20 m below datum at Blank Island, Ketchikan, Alaska; 6 June 1987, one specimen 11 mm long, 5 m below datum at Clover Island, Ketchikan, Alaska; 7 June 1987, one specimen 11 mm long, 20 m below datum at Cutter Rock, Ketchikan, Alaska, deposited as a voucher specimen in the Royal British Columbia Museum, RBCM 988.24.1; 8 June 1988, 3 specimens, 6, 7.5 and 8 mm long, collected with spawn, 17 m below datum at Porlier Pass, Galiano Island, British Columbia (49°01'N, 123°36'W) on the hydroid *Sertularella* sp. All specimens were collected by the author on rocky substrates and length measurements are of live animals.

Anatomy: The living animal is moderately stout (Figure 2) and up to 11 mm in length. The body color is translucent white with opaque white ovotestis and oral glands, brown jaws, and black eyes visible through the skin. The oral tentacles taper and are slightly flattened dorsoventrally. They arise from the top anterolateral corners of the head. The smooth, cylindrical, tapering rhinophores are slightly longer than the oral tentacles. Both rhinophores and tentacles are encrusted with opaque white pigment dorsally. The head is subglobular with a T-shaped mouth opening.

The cerata are stout and slightly bulbous or cylindrical, with the tips abruptly forming a small point. Inside are large white cnidosacs. The liver diverticula are pale or dark olive green with darker granulations. The diverticula fill most of the interior of each ceras. The ceratal sheath is transparent. Each ceras bears opaque white pigment spots concentrated into two broken longitudinal lines on either side of its anterior face. The anterior face of each ceras is suffused with an opalescent orange blush of pigment which is more concentrated near the cnidosac base.

The cerata are arranged in distinct, almost vertical, rows borne on slight elevations. There are 4 or 5 pre-cardiac and 6 or 7 post-cardiac rows on either side of the animal, with up to 8 cerata per row. The short anteriormost row is a branch of the second row. The acleioproct anus is posterior in the interhepatic space, in front of the gap between the innermost two cerata of the first post-cardiac row. The gonopore is below and slightly posterior to the second or third ceratal row of the right anterior liver branch.

The foot is truncated, thickened anteriorly, and expanded slightly to form rounded corners. It has a small flange and ends in a short, bluntly pointed tail, which has an opaque white stripe in most specimens.

The uniserrate radula contains 45–58 teeth. The central cusp is equal in length to the first of the five or six denticles

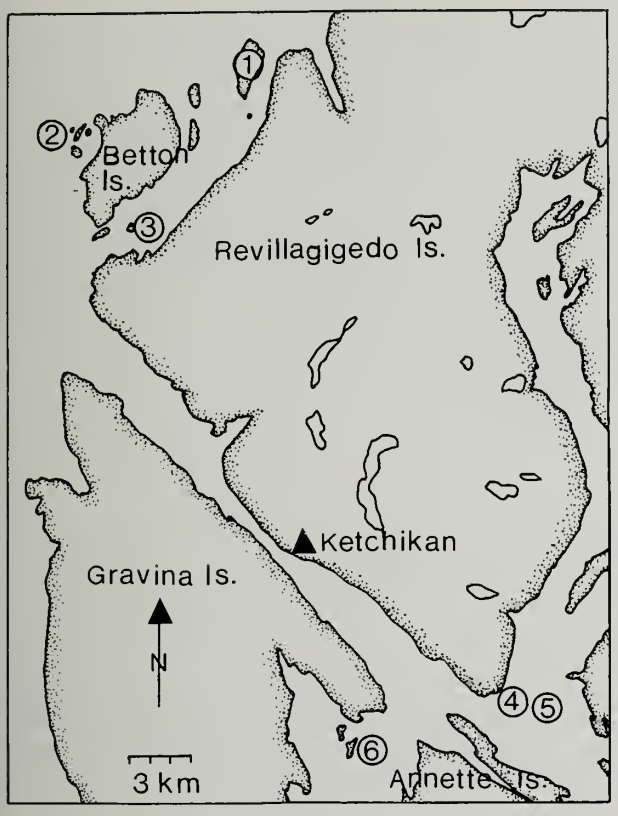

Figure 1

Map of Ketchikan, Alaska, showing collection sites: 1, Grant Island; 2, Tatoosh Islands; 3, Clover Island; 4, Mountain Point; 5, Cutter Rock; 6, Blank Islands.

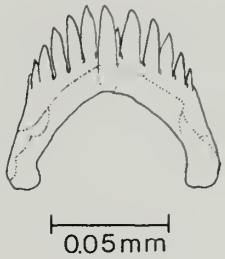

Figure 3

Radular tooth of *Cuthona viridis*.

on each side (Figure 3).There is sometimes a small intermediate denticle on one side of the central cusp. The width of the ribbon in an 8-mm specimen increased from 49 to 86 μm. In an 11-mm specimen the largest tooth was 98 μm wide and 86 μm high. The elongate jaws (Figure 4) have a large, delicate, masticatory flange, which has an irregular edge, but no obvious denticulations.

Small salivary glands are located on both sides of the esophagus. Large, straplike oral glands, with numerous short, fluffy white side branches, fill the anterior end of the animal.

In the reproductive system (Figure 5A), the ovotestis is connected by the preampullary duct to a kidney-shaped ampulla. The narrow postampullary duct branches to form a short oviduct, entering the female gland mass, and a narrow vas deferens. The vas deferens enlarges into a prostatic portion, folds back on itself and then curves and narrows into a non-prostatic portion, which enters the

Figure 2

Cuthona viridis, drawn from a photograph of a live animal, 11 mm long.

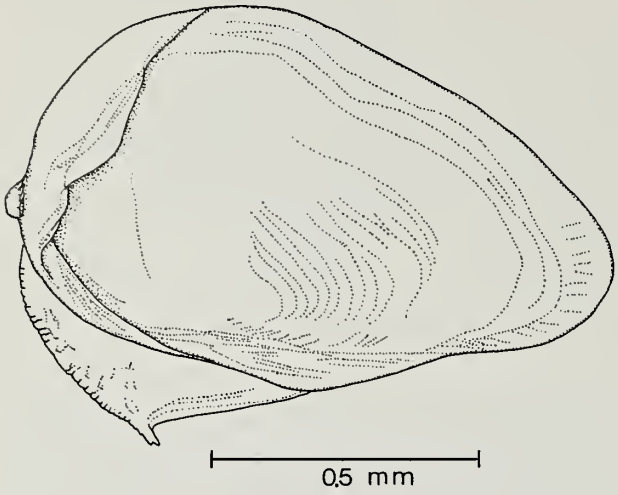

Figure 4

Jaw of *Cuthona viridis*.

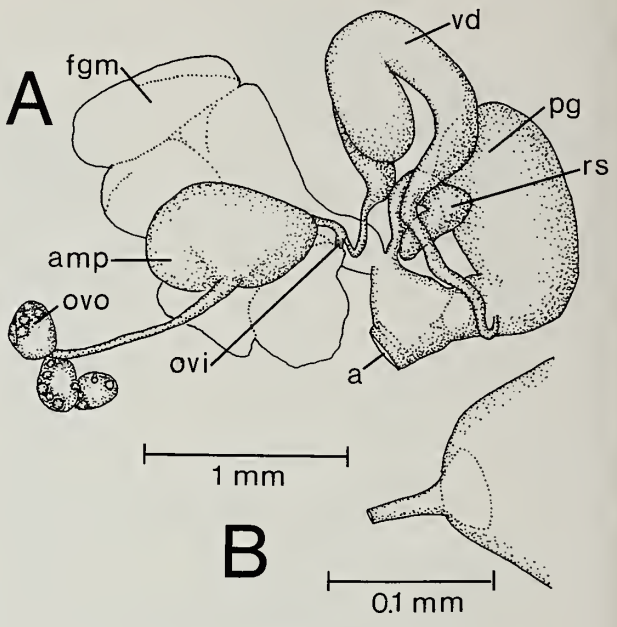

Figure 5

A. *Cuthona viridis* reproductive system from a camera lucida drawing. Key: a, common aperture; amp, ampulla; fgm, female gland mass; ovi, oviduct; ovo, ovotestis; pg, penial gland; rs, receptaculum seminis; vd, vas deferens. B. Penial stylet.

penial sac at the junction of the large, unstalked penial gland. The penis bears a golden-brown, straight, conical stylet (Figure 5B). There is an elongate, short-stalked receptaculum seminis, which is recurved, appearing as a spherical mass. It is located near the junction of the common genital atrium.

Spawn masses are upright ribbons, 1.5 mm high, laid in one and one-half coils. They contain capsules with a mean length of 171 μm, each with one white egg having a mean diameter of 134 μm.

RANGE EXTENSIONS

The following species are listed in alphabetical order with the new range marked by an asterisk. The changed northern range limit and its reference follow in parentheses.

Adalaria sp.—*Tatoosh Island, Ketchikan, Alaska to North Cove, Cape Arago, Oregon (British Columbia; MILLEN, 1987).

Ancula pacifica MacFarland, 1905—*Grant Island, Ketchikan, Alaska to Point Loma, San Diego, California (Bamfield, Vancouver Island, British Columbia; MILLEN, 1983).

Aplysiopsis smithi (Marcus, 1961)—*Cutter Rock, Ketchikan, Alaska to San Diego, California; Bahía de Los Angeles to Bahía de San Carlos, Gulf of California, Mexico (Crescent Beach, British Columbia; MILLEN, 1980).

Catriona columbiana (O'Donoghue, 1922)—*Cutter Rock, Ketchikan, Alaska to Mission Bay, San Diego, California; Japan; Capetown, South Africa (Pearse Island, British Columbia; LAMBERT, 1976).

Cuthona viridis (Forbes, 1840)—N.E. Pacific: *Blank Island, Ketchikan, Alaska to Porlier Pass, Galiano Island, British Columbia; Boreal amphi-Atlantic (first Pacific records).

Dendronotus diversicolor Robilliard, 1970—*Cutter Rock, Ketchikan, Alaska to Point Loma, San Diego, California (Porcher Island, British Columbia; LAMBERT, 1976).

Diaphorodoris lirulatocauda Millen, 1985—*Clover Island, Ketchikan, Alaska to Punta Banda, Baja California, Mexico (Juan Perez Sound, Queen Charlotte Islands; MILLEN, 1985).

Discodoris heathi MacFarland, 1905—*Cutter Rock, Ketchikan, Alaska to Bahía San Quentín, Baja California, Mexico (Porcher Island, British Columbia; LAMBERT, 1976).

Doto amyra Marcus, 1961—*Blank Island, Ketchikan, Alaska to Ensenada, Baja California, Mexico; Puerto Peñasco, Sonora, Mexico (Port Hardy, Vancouver Island, British Columbia; MILLEN, 1983).

Eubranchus olivaceus (O'Donoghue, 1922)—*Grant Island, Ketchikan, Alaska to Asilomar Beach, California; (Nuchatlitz Island, Esperanza Inlet, Vancouver Island, British Columbia; MILLEN, 1983).

Eubranchus rustyus (Marcus, 1961)—*Mountain Point, Ketchikan, Alaska to Punta Abreojos, Baja California, Mexico (Stubbs Island near Telegraph Cove, Vancouver Island, British Columbia; MILLEN, 1983).

Eubranchus sanjuanensis Roller, 1971—*Mountain Point, Ketchikan, Alaska to San Juan Island, Washington; northern New England (Porlier Pass, Galiano Island, British Columbia; MILLEN, 1983).

Flabellina pricei (MacFarland, 1966)—*Mountain

Point, Ketchikan, Alaska to La Jolla Canyon, San Diego, California (Pearse Island, British Columbia; LAMBERT, 1976).

Hallaxa chani Gosliner & Williams, 1975—*Grant Island, Ketchikan, Alaska to La Jolla, California (Earl's Cove, Agamemnon Channel, British Columbia; MILLEN, 1983).

Polycera (*Palio*) *zosterae* O'Donoghue, 1924—*Cutter Rock, Ketchikan, Alaska to Bodega Bay, California (Shushartie Bay, Vancouver Island, British Columbia; ROBILLIARD, 1971).

Stiliger fuscovittatus Lance, 1962—*Cutter Rock, Ketchikan, Alaska to San Diego, California; Bahía de los Angeles, Baja California, Mexico (Flat Top Islands, British Columbia; MILLEN, 1980).

DISCUSSION

This paper presents an expanded description of *Cuthona viridis* because it has not previously been recorded in the Pacific, and Pacific specimens differ in a few minor aspects from published accounts of Atlantic animals. Externally, the Alaskan specimens more closely resembled the drawing by Lemche in JUST & EDMUNDS (1985:pl. 59E–G) than the drawings by BROWN (1980:fig. 3I–K). Color differences are minor: the anterior ceratal faces had an orange rather than a yellow suffusion and the opaque white spots form two longitudinal streaks rather than one streak below a subapical ring as reported by THOMPSON & BROWN (1984). The cerata are distinctive in that they are stout compared with other tergipedids and have blunt ends, with wide cnidosacs and tiny, pointed tips. The cerata are borne on distinct, widely separated, almost vertical rows upon somewhat raised portions of the notum. The ceratal pattern is similar to that drawn by LEMCHE (1941:fig. 2). The row posterior to the anus did not fork as in the specimens drawn by ODHNER (1939:fig. 37).

The major internal difference is that the masticatory edge of the jaw is irregular but not denticulate. The reproductive system is as drawn by ODHNER (1939:fig. 40) except that the receptaculum seminis is a recurved tube rather than spherical and there is a common atrium. Both of these features are illustrated by LEMCHE (1941:fig. 2). There is a dark straight, conical penial stylet as mentioned by LEMCHE (1941) and BROWN (1980). The spawn mass is shorter but similiar in shape to that illustrated in KRESS (1971) and the eggs are the same size.

MILLER (1977), BROWN (1980) and THOMPSON & BROWN (1984) compare *Cuthona viridis* with *C. albocrusta* (MacFarland, 1966), *C. signifera* (Baba, 1961) and *C. scintillans* Miller, 1977. MILLER (1977) discussed several differences and it does not appear that these species are synonymous. The sympatric *C. albocrusta* differs externally in having more bluntly ended tentacles and rhinophores. The ceratal rows begin considerably farther behind the rhinophores, are more closely spaced, and are not raised. The cerata are more inflated and have smaller cnidosacs. The white encrustations on the cerata are not in the form of large white spots or streaks. Internally it differs in having narrower radular teeth with fewer denticles per side and possessing sharp denticulations on the jaw. The reproductive system has the vas deferens and penial sac joining the penis near its tip rather than its base, and has a curved as opposed to a straight penial stylet. The spawn mass is sausage-shaped, rather than the upright ribbon laid by *C. viridis*.

The presence of *Cuthona viridis* in the boreal northeastern Pacific and boreal amphi-Atlantic is not an uncommon pattern for opisthobranch mollusks. At present, 17 other opisthobranch species are known to share this type of distribution—which raises interesting questions. Are the populations discontinuous, or could there be gene flow through the Arctic, possibly during the summer, in El Niño years? If the populations are discontinuous, as low temperature and low salinity barriers suggest, how long have they been so, and why has speciation not taken place? A better understanding of geographical distributions may help to provide some answers.

ACKNOWLEDGMENTS

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The Nudibranch *Halgerda aurantiomaculata* (Allan, 1932) (Doridoidea: Doridiidae) in Fijian Waters

by

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Abstract. *Halgerda aurantiomaculata* (Allan, 1932) was previously known from shelf waters of Queensland and southeastern Papua New Guinea, but new records from Fiji and the southern Coral Sea (Lord Howe Island and Elizabeth Reef) indicate a considerably larger natural distributional range. An account of the anatomy, particularly that of the gut and reproductive system, of the Fijian specimens is provided and is consistent with that of Queensland material with which it was compared. This comparison, however, brought to light errors in the original description regarding the size, radular formula, and tooth structure of the holotype. The extent of intraspecific color variation within *H. aurantiomaculata* is reported; this variation is apparently continuous. Character states present in *H. aurantiomaculata* are used to test pre-existing criteria for definition of the genus *Halgerda*; five are supported and two are invalidated.

INTRODUCTION

Two specimens of the dorid nudibranch *Halgerda aurantiomaculata* (Allan, 1932) have recently been collected on the southern coast of Viti Levu, the largest island in the Fijian archipelago. Previously *H. carlsoni* Rudman, 1978, was the only *Halgerda* recorded from this area. *Halgerda aurantiomaculata* had formerly only been reported from the shelf waters of Queensland and southeastern Papua New Guinea. Its discovery in Fiji represents a range extension of approximately 2500 km eastwards into the central-west Pacific Ocean.

This identification was confirmed through examination of the holotype of *Dictyodoris aurantiomaculata* Allan, 1932.

During the course of our study of the Fijian specimens, colleagues informed us of two additional, significant records from the southern Coral Sea—from Lord Howe Island and Elizabeth Reef. We examined both animals and can confirm they are *Halgerda aurantiomaculata.*

All measurements of length given in the following description relate to the fully extended crawling state unless otherwise specified.

TAXONOMY

Halgerda aurantiomaculata (Allan, 1932)

(Figures 1–22, 25–32)

Synonymy:

Dictyodoris aurantiomaculata ALLAN, 1932:91, pl. 4, figs. 7, 8, pl. 5, figs. 8–10; KENNY, 1960:225; BURN in Thompson, 1975:515.

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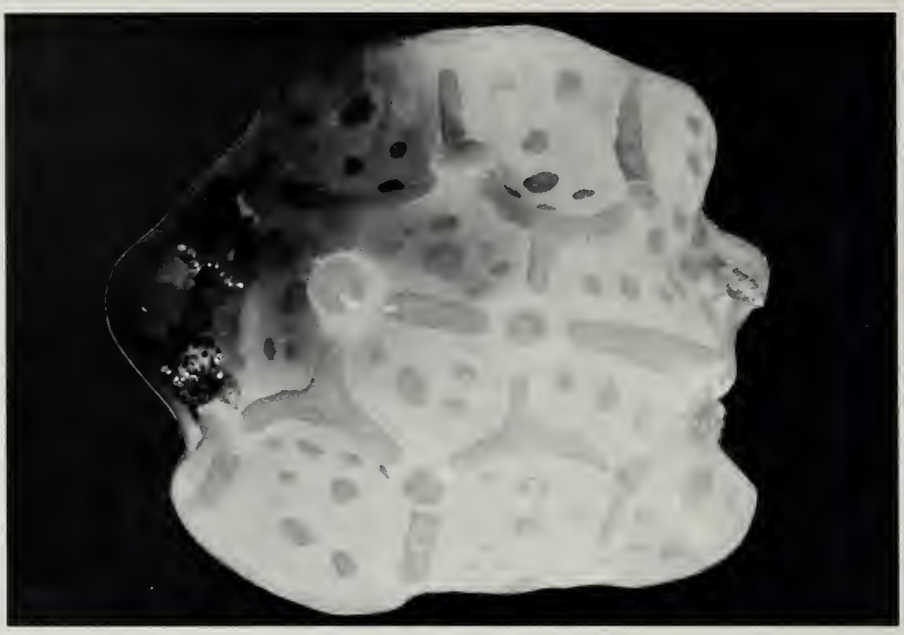


Figure 1

Halgerda aurantiomaculata. First specimen, photographed soon after preservation; length 24 mm. From 24 m, Suva Harbour Channel, Laucala Bay, southern coast of Viti Levu Island, Fiji, 25 June 1987. Photograph: R. C. Willan.

Asteronotus brassica; GILLETT & MCNEILL, 1959, pl. 84—top right; GEORGE & GEORGE, 1979:98, pl. 92, fig. 4 (misidentification—not *Asteronotus brassica* Allan, 1932).

Halgerda aurantiomaculata (Allan); COLEMAN, 1975:129; RUDMAN, 1978:84; ENDEAN, 1982:144, no. 156; BERTSCH & JOHNSON, 1982:217; WILLAN & COLEMAN, 1984:38–39, 52.

Material examined: FIJI: 1 specimen, 24 m, Suva Harbour channel, southern coast of Viti Levu Island, Fiji (18°08′S, 178°25′E), J. Brodie, 25 June 1987; 1 specimen, 11 m, "The Amphitheater," Beqa (=Mbegga) lagoon, southern coast of Viti Levu Island, Fiji (18°24′S, 178°00′E), G. Brodie, 16 January 1988. AUSTRALIA: Holotype, collected intertidally, North West Island, Capricornia Section, Great Barrier Reef, central Queensland (23°18′S, 151°42′E), "Master" Embury, January 1931, The Australian Museum, Sydney, Reg. No. C57208; 22 specimens, from Lizard Island (14°40′S, 145°28′E) to Cape Moreton (27°11′S, 153°24′E), Queensland, 1980 to 1987. LORD HOWE ISLAND: 1 specimen, 10 m, Malabar (31°17′S, 159°05′E), N. Coleman, 28 November 1979, Museum of Victoria, Melbourne, Reg. No. F30126. ELIZABETH REEF, SOUTHERN CORAL SEA: 1 specimen, 20 m, SE outer slope (29°58′S, 159°05.1′E), P. Hutchings, 12 December 1987, The Australian Museum, Sydney, Reg. No. C155069. PAPUA NEW GUINEA: 1 specimen, 15 m, Horseshoe Reef, Port Moresby (9°30′S, 147°10′E), N. Coleman, August 1980, Museum of Victoria, Melbourne, Reg. No. F30127.

DESCRIPTION OF FIJIAN SPECIMENS

(Figures 1–8, 25–27)

The two animals measured 30 and 35 mm long alive, and 24 and 27 mm long respectively after preservation. In life, the body was low in profile and oval in outline; the mantle margins were straight instead of undulating as they were in the freshly preserved animal (Figure 1). The expansive mantle was gelatinous yet firm and it completely lacked spicules. The mantle in both specimens bore 10 prominent, rounded pustules. Four pustules were present along the midline, one (the smallest of all 10) immediately in front of the rhinophores, and three, equally spaced, between the rhinophores and gills. A mid-dorsal ridge connected these pustules and it stopped abruptly at the last pustule, *i.e.*, it did not extend from there to the branchial pocket. Two additional rows, each consisting of three pustules, were present on the flanks of the mantle, one on either side of the median row. Pustules within these lateral rows were arranged symmetrically, both with respect to each other and to the median row; that is, each pustule was displaced one-half the inter-pustule distance of the median row, so that the posterior one was situated in line with the branchial pocket. Both the rhinophoral and branchial pockets had elevated rims with simple margins. The foot was much narrower than the mantle (*i.e.*, the foot of the first specimen measured 3 mm in width against a mantle width of 19 mm in the preserved state). The foot was bilaminate an-

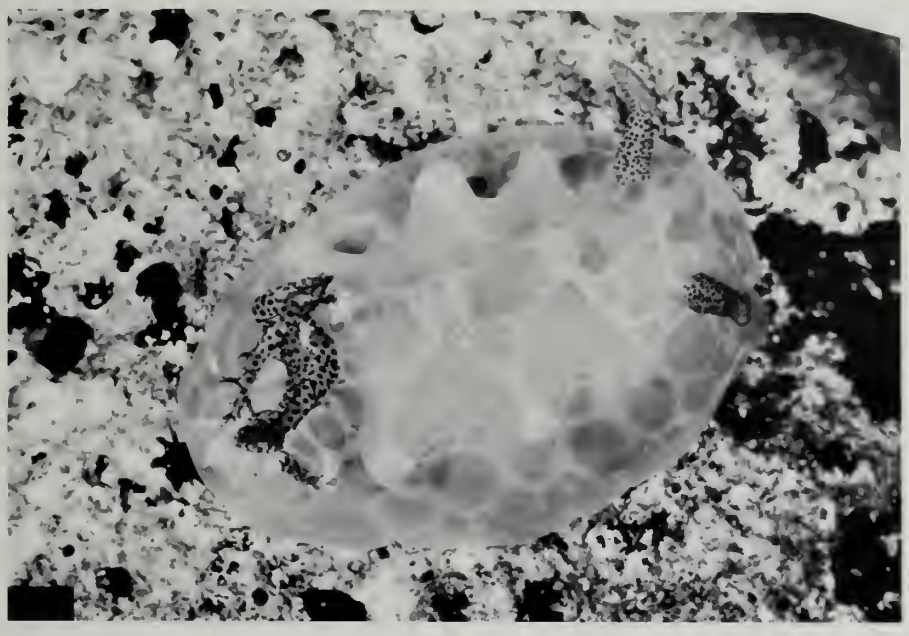


Figure 2

Halgerda aurantiomaculata. Second specimen, photographed live; length 35 mm. From 11 m, "The Amphitheater," Beqa lagoon, southern coast of Viti Levu Island, Fiji, 16 January 1988. Photograph: J. Brodie.

teriorly, the anterior lamina being vertically notched and the posterior lamina transversely grooved in the midline. Short, triangular oral tentacles were present on either side of the head, and there was no indication of a posterior longitudinal groove in the oral tentacles of either specimen. The rhinophores were relatively tall and tapering, the stalk was elongate, and the small, backwardly tilted clavus, which bore about 25 lamellae, was approximately equal in maximum diameter to the base of the stalk. The four gills were sparsely bipinnate, the posterior two being split into two branches from near their base.

The body was opaque white, almost hyaline, and all 10 pustules were capped with a vivid orange spot. Orange streaks marked the summits of the ridges and these intersected to produce two Y- or V-shaped, broad patches transversely on either side of the midline. In addition, orange streaks radiated towards the margin from each lateral pustule. The mantle margin possessed a continuous, narrow, orange line. Orange spots of differing sizes were present on the mantle surface in the flat-bottomed depressions between the ridges; there were three to eight spots in each depression. The rhinophoral stalks and the lamellae on the clavi bore numerous small, rounded, regularly spaced chocolate brown spots, those on the stalk being darker and slightly larger. The base of the branchial pocket and gill rachis also possessed several relatively large, dark chocolate brown spots. The gills themselves were densely pigmented with much smaller brown spots giving a densely speckled appearance. The anal papilla was brown spotted. The foot possessed a continuous orange marginal line. Both the oral tentacles had an orange spot at their apex. Only the second specimen had any orange pigmentation around its genital aperture.

The viscera were surrounded by a thin, translucent tissue envelope which was pale brown because of numerous light brown pigment specks; this sheath was so transparent that the organs of the viscera could be recognized through it. Dorsally, the oesophagus, stomach, rectum, and digestive gland were immediately identifiable when the mantle and this tissue envelope were opened by a mid-dorsal longitudinal incision and folded aside. A composite view of the digestive system is shown in Figure 3. The foregut, which is shown in profile in Figure 3, consisted of a long and muscular oral tube with three prominent extrinsic retractor muscles on either side, a muscular pharyngeal bulb with two posterolateral bulges, an extremely large and curved radular sac, and a thin-walled oesophagus. The two dorsal pairs of retractors originated from the mantle; in fact the uppermost pair originated from the region where the anteriormost pustule in each lateral row was present on the outer surface. The ventral pair of retractors originated from the foot musculature. The large stomach was spherical and thin-walled, and it gave rise to the long intestine anteriorly. The stomach and hindgut are shown in dorsal view in Figure 3. The digestive gland formed a large, ovoid, compact, cream-color mass in the middle of the visceral cavity.

Dissolution of the pharyngeal bulb yielded a lightly

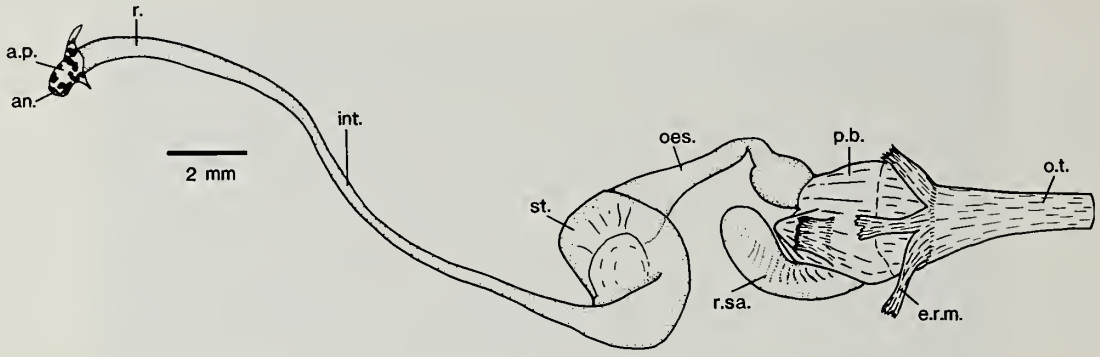


Figure 3

Composite view of structure of alimentary canal of Fijian *Halgerda aurantiomaculata* (digestive gland omitted). Abbreviations: an., anus; a.p., anal papilla; e.r.m., extrinsic retractor muscle (lowest of three indicated); oes., oesophagus; int., intestine; o.t., oral tube; p.b., pharygeal bulb; r., rectum; r.sa., radular sac; st., stomach.

cuticularized labial ring and a broad, elongate radula, but no jaws. The radulae of the two specimens measured 4.9 and 6.2 mm long by 3.6 and 4.8 mm in maximum width respectively when spread out and laid flat on slides. The radular formulae were 50 × 51·0·51 and 48 × 47·0·47 respectively. The radular teeth were numerous and crowded together, and all possessed a simple, hooked form. The innermost 20 to 25 teeth (Figure 25) had short, broad blades arising from very elongate basal plates; the row of basal plates was inclined at a steep angle to the midline of the radula; these teeth were relatively minute, with vertical height increasing progressively from a minimum of 12 μm at tooth number 1. Middle (Figure 26) and outer lateral teeth were arranged in straight rows; all these teeth were alike, consisting of a relatively tall (average vertical height 145 μm), gently curved cusp and narrow, almost rectangular basal plate. All the lateral teeth possessed a strong flange from the base to about halfway up the blade on the inner margin. The five outermost teeth in a row decreased rapidly in size, and there were one or two ad-

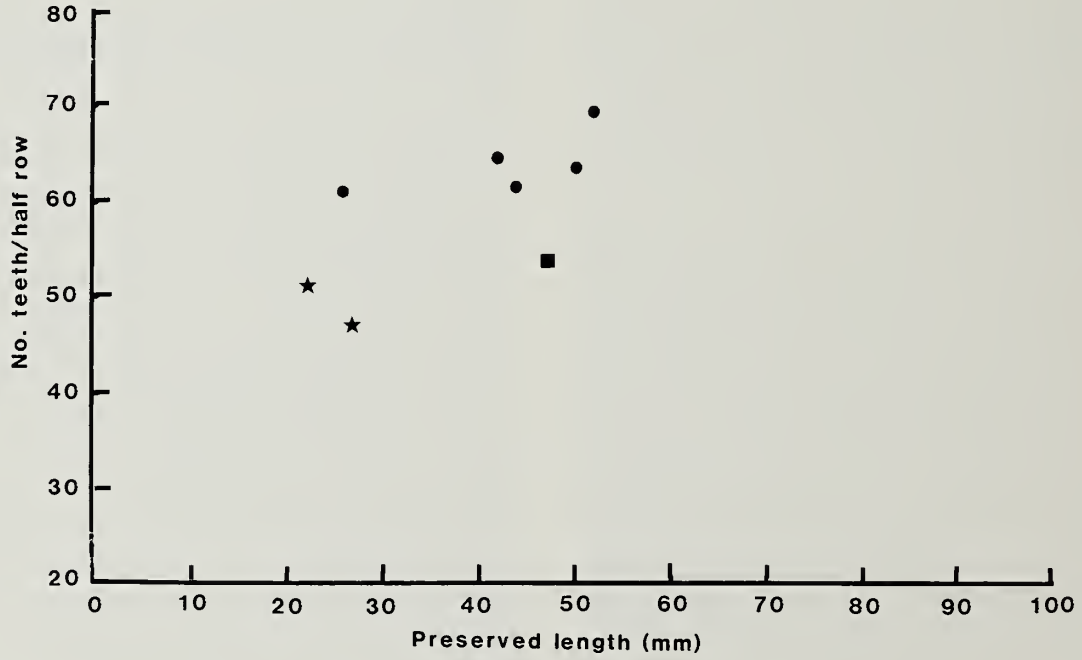


Figure 4

Halgerda aurantiomaculata. Graph showing relationship between preserved length and number of teeth per half row. Data points from five Queensland specimens (●), holotype (■), and two Fijian specimens (★).

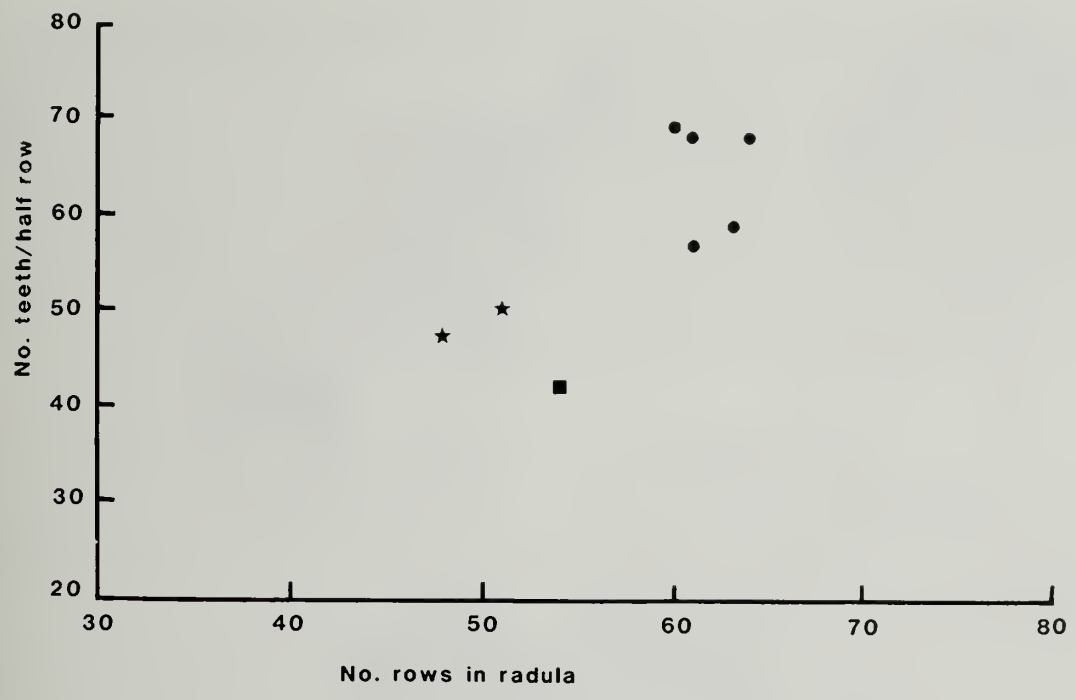
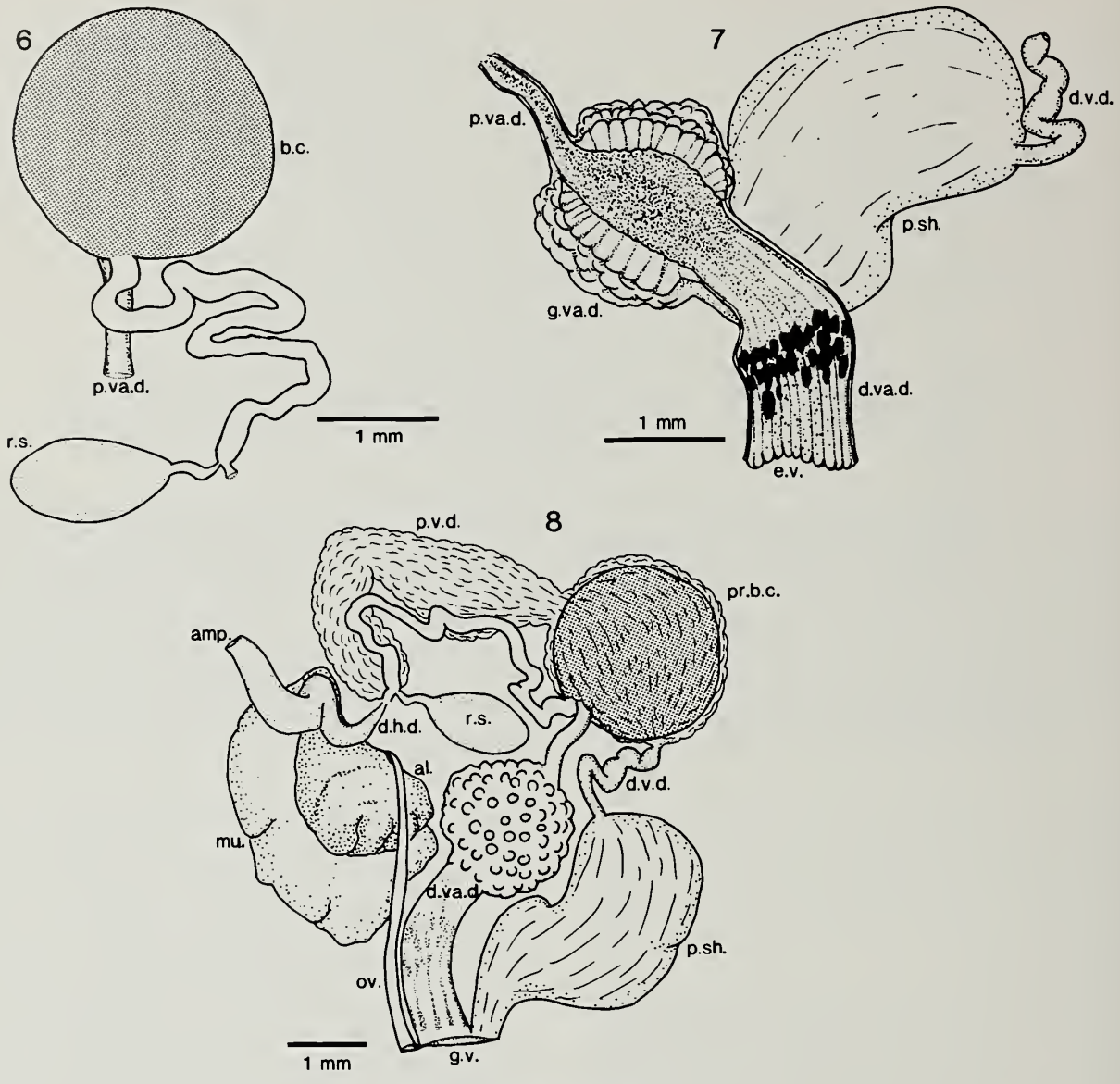


Figure 5

Halgerda aurantiomaculata. Graph showing relationship between number of rows in radula and number of teeth per half row. Same symbols for data points as in Figure 4.

ditional much reduced, extreme outer laterals in most rows. Of these reduced outermost laterals, the extreme outermost tooth (number 51) was deeply, and the two teeth next to that (numbers 49 and 50) weakly, bifid on both halves of the radula of one (Figure 27), but not the other, Fijian specimen's radula.

The triaulic reproductive system consisted of a relatively small anterior genital (strictly gonoducal) mass compared to the entire visceral space. The only organ prominent dorsally was the prostate-ensheathed bursa copulatrix, this organ being located below, and to the right of, the oesophagus. The large, bright orange-yellow ovotestis overlaid the digestive gland dorsally in the posterior half of the visceral cavity and developing ova were clearly visible within the ovotestis. The relatively short ampulla left the ovotestis and passed almost directly to the anterior genital mass which it entered beside the nidamental glands. Within the anterior genital mass, it gradually narrowed into an hermaphroditic duct which was connected to the bursa copulatrix and prostate gland, but these connections were so fine they could not be traced without sectioning. The duct to the bursa was long and sinuous, and a smaller, thicker-walled, clublike receptaculum seminis arose by a short and narrow stalk exactly at the point this duct entered the nidamental glands. The bursa (Figure 6) itself was spherical, thin-walled, and filled with brown flocculent material; it was approximately equal to the penial sheath in size. A thin-walled proximal vaginal duct left the bursa, suddenly dilated into an obvious, lobular, glandular middle section, and passed to the exterior via a relatively long, broad, distal vaginal duct. Internally, the distal vagina possessed about 12 strong, longitudinal ridges and a conspicuous superficial band of chocolate brown spots (Figure 7). The vas deferens enlarged immediately upon leaving the hermaphroditic duct into a white, lobulate, prostatic proximal section that was both folded once back upon itself and compressed between the nidamental glands and penial sheath. The central section of the vas deferens remained enlarged and lobulate, and it entirely ensheathed the bursa except for a small area where the hermaphroditic duct and proximal vaginal duct entered side by side. The vas deferens darkened from white to pale brown immediately prior to its distal section. Distally, the vas deferens narrowed rapidly and was somewhat sinuous before it entered the large, muscular penial sheath. There was no penial armature. Although the distal vagina and ejaculatory duct opened into a common vestibule, they both possessed completely separate canals. Two separate glands could be discerned within the nidamental mass: a smaller, more solid, creamish albumen gland and a larger, white mucus gland. In the retracted state, the oviduct opened at the genital aperture immediately behind the vestibule of the vagina and ejaculatory duct. Figure 8 illustrates a composite view of the structure of the unravelled reproductive organs.



Explanation of Figures 6 to 8

Reproductive system of Fijian *Halgerda aurantiomaculata.*

Figure 6. Detail of seminal receptacles (prostate gland removed from outside of bursa copulatrix).

Figure 7. Detail of vagina and terminal male tract (vagina opened longitudinally throughout its length to show internal structures; penial sheath not removed).

Figure 8. Composite view of structure of reproductive organs.

Abbreviations: al., albumen gland; amp., ampular region of hermaphroditic duct; b.c., bursa copulatrix; d.h.d., distal hermaphroditic duct; d.va.d., distal vaginal duct; d.v.d., distal vas deferens; e.v., entrance to vagina; g.va.d., spherical, glandular central section of vagina; g.v., genital vestibule; mu., mucus glands, ov., oviduct; pr.b.c., central section of prostate gland ensheathing bursa copulatrix; p.sh., penial sheath; p.va.d., proximal vaginal duct; p.v.d., proximal vas deferens; r.s., receptaculum seminis.

COMPARISON WITH EASTERN AUSTRALIAN SPECIMENS

To confirm the identity of the Fijian *Halgerda* specimens, it was necessary to check them against material of *H. aurantiomaculata* from eastern Australia, not only to fill gaps in ALLAN's (1932) original description, but also to consider intraspecific variation. The results of this examination and comparison are given below under five subheadings. This consideration has been extended to cover what is now known of other tropical Indo-Pacific *Halgerda*

species (Rudman, 1978; Bertsch & Johnson, 1982; Willan & Coleman, 1984; Gosliner, 1987).

External Morphology

All specimens of *Halgerda aurantiomaculata* possess the same oval outline and gelatinous yet firm mantle texture. Adults can attain 70 mm maximum crawling length. The holotype measures 47 mm preserved, not 77 mm as erroneously stated in the original description. There is apparently no variation in arrangement of the 10 large pustules or system of semi-interconnecting ridges. As Bertsch & Johnson (1982) noted, the median row of four pustules with their low connecting ridge is specifically characteristic for *H. aurantiomaculata*. The only intraspecific differences we noted were the relative heights of pustules within and between individuals. Sometimes all the pustules are very pronounced (Figures 11, 14, 20–22) and sometimes they are all low (Figures 13, 15, 17, 18). The anteriormost pustule in the median set is generally lower than the three others, or it may be barely present at all (see Figure 2 for example).

Of the other described species of tropical Pacific *Halgerda,* only *H. carlsoni* Rudman, with type locality of Fiji, has similar shape and ornamentation. However that species (Figures 23, 24) possesses about 40 additional pustules of varying size connected into the major pustule and ridge system on the mantle. In *H. carlsoni* there are fewer, larger, chocolate spots on the rhinophoral stalk and clavus. Both *H. aurantiomaculata* and *H. carlsoni* have similar rhinophores consisting, when fully extended, of a tall stalk that is approximately equal in diameter to the maximum diameter of the elongate, tapering clavus (Figures 13 and 23 respectively).

Coloration

The extent of intraspecific color variation present within *Halgerda aurantiomaculata* has not been understood previously. Figures 9 to 22 depict this variation in eastern Australian material. "Typical" specimens (*i.e.,* those matching the holotype) have about 100 rich-orange spots on the mantle. Figure 10 illustrates a specimen like this. Not only does the number of spots vary, but so does their size; some individuals have large spots that nearly coalesce to leave only small translucent white "pathways" between them (Figures 12, 16), while others, particularly juveniles, are predominantly translucent white with much smaller spots (Figures 17, 18, 22). The summits of all 10 pustules are always orange. The ridges connecting the pustules, as well as those radiating from the two lateral rows of pustules, are usually capped by an orange streak that can be either wide or narrow. When they are wide, they resemble the spots on the rest of the mantle (Figures 12, 13, 16), and this is the case with the second Fijian specimen (Figure 2). When they are narrow, they create a distinctly geometric appearance. The first Fijian specimen is like this (Figure 1) as is one specimen from Heron Island, southern Great Barrier Reef (Figure 20). This latter animal is interesting because it has very few orange spots. This streaked morph, then, appears to represent one end point to the range of coloration. Color variation seems to be continuous between all morphs, but the streaked morph appears to be the rarest.

Halgerda carlsoni Rudman, *H. terramtuentis* Bertsch & Johnson, and the undescribed Queensland species illustrated by Willan & Coleman (1984:species number 117) all also possess orange caps to the pustules but lack the additional large spots on the mantle as found in *H. aurantiomaculata.*

Alimentary Canal

The gut of the Fijian specimens (Figure 3) was identical in all respects to that of two Queensland animals dissected to reveal this system. The most characteristic regions were the elongate and unspotted oral tube, enlarged and curved radular sac, posteriolateral bulges to the pharyngeal bulb, large dorsal stomach, and brown-spotted anal papilla.

It is impossible to decide from literature whether all these characteristics relating to the gut hold true just for this species or whether they are to be found in all species of the genus. Rudman (1978:83–84) indicated that the enlarged, curved radular sac and large stomach were typical of the genus. However, he also suggested that the tissue envelope surrounding the viscera should be very dark brown or black in all species of *Halgerda* (Rudman, 1978:83), but it is, in fact, translucent in at least two species, *H. carlsoni* (Rudman, 1978:83) and *H. aurantiomaculata* (present observations).

Radula

The radula of the Fijian specimens (Figures 25–27) is identical to that of the five Queensland specimens (Figures 28–32) whose radula we prepared for examination. The majority of radular teeth are simple with an apical cleft occurring in the reduced outermost marginals in most specimens. This cleft was absent in one Fijian and one Queensland (Figure 32) specimen.

In her description, Allan (1932) stated that the teeth were "slightly denticulate" but she illustrated three simple teeth (Allan, 1932:pl. 5, fig. 10), the two on the left being superimposed (and resembling incompletely cuticularized ones from the growing end of the radula). It seems likely that Allan misinterpreted these two simple teeth as one single, denticulate tooth because there is no indication of denticles on any tooth in her illustration.

The matter of observation of the structure of the teeth is not the only anomaly in Allan's (1932) original description of the radula of *Halgerda aurantiomaculata.* For an animal its size, the radular formula given by Allan of 42 × 54·0·54 is consistently below that of all the other specimens we examined (Figures 4, 5). Our re-examina-

tion of the holotype provided an explanation. Its buccal mass was never treated to isolate the radula, but the buccal mass had been sagittally sectioned instead. Therefore the radula remains in place on the muscular odontophore, but the elongate radular sac had been cut off posteriorly. We assume the radular sac had been accidentally excised during removal of the buccal mass. Consequently, Allan's formula fails to take account of the rows of teeth in the radular sac. We stained the entire buccal mass of the holotype while still *in situ* and were able to count approximately 60 teeth in each half row.

Reproductive System

The Fijian specimens exactly matched the three Queensland specimens that we dissected in all the characters of the reproductive system except that, being smaller in overall body length, the ovotestis overlaid only a smaller section of the digestive gland.

The reproductive system appears to offer a great many comparative characters, at both specific and generic levels. The most distinctive features in the reproductive system of *Halgerda aurantiomaculata* are to be found within the

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Explanation of Figures 9 to 16

Variation in *Halgerda aurantiomaculata.*

Figure 9. Length 68 mm. From 10.5 m, Flinders Reef, north of Cape Moreton, southern Queensland, 31 March 1984. Photograph: R. C. Willan.

Figure 10. Length not recorded. From 9 m, Wistari Reef, Great Barrier Reef, central Queensland, July 1980. Photograph: K. Tubbenhauer.

Figure 11. Length not recorded. From 12 m, Heron Island, Great Barrier Reef, central Queensland, August 1978. Photograph: J. C. Paterson.

Figure 12. Length 59 mm. From 9 m, Fantome Island, Palm Isles Group, northern Queensland, 23 March 1982. Photograph: R. C. Willan.

Figure 13. Length 42 mm. From 21 m, Lady Musgrave Island, southern Queensland, April 1986. Photograph: C. Buchanan.

Figure 14. Length not recorded. From 7 m, Brittomart Reef, Great Barrier Reef, northern Queensland, 29 November 1984. Photograph: D. J. Brunckhorst.

Figure 15. Length 60 mm. From 12 m, Lady Musgrave Island, southern Queensland, April 1986. Photograph: C. Buchanan.

Figure 16. Length 41 mm. From 9 m, Wistari Reef, Great Barrier Reef, central Queensland, 3 September 1983. Photograph: R. C. Willan.

Explanation of Figures 17 to 24

Variation in *Halgerda* species.

Figure 17. *H. aurantiomaculata.* Length 21 mm. From 10.5 m, Heron Island, Great Barrier Reef, central Queensland, 15 November 1980. Photograph: R. C. Willan.

Figure 18. *H. aurantiomaculata.* Length 21 mm. From 9 m, Flinders Reef, north of Cape Moreton, southern Queensland, 23 August 1980. Photograph: R. C. Willan.

Figure 19. *H. aurantiomaculata.* Length 58 mm. From 7.5 m, Wistari Reef, Great Barrier Reef, central Queensland, 6 July 1981. Photograph: R. C. Willan.

Figure 20. *H. aurantiomaculata.* Length not recorded. From Heron Island, Great Barrier Reef, central Queensland, December 1981. Photograph: N. Coleman.

Figure 21. *H. aurantiomaculata.* Length 66 mm. From 6 m, Wistari Reef, Great Barrier Reef, central Queensland, 30 November 1987. Photograph: D. J. Brunckhorst.

Figure 22. *H. aurantiomaculata.* Length 64 mm. From 10 m, Heron Island, Great Barrier Reef, central Queensland, 28 November 1987. Photograph: D. J. Brunckhorst.

Figure 23. *H. carlsoni,* paratype. Length not recorded. From 3 to 6 m, Admiralty Island, Bay of Islands, Suva Harbour, Viti Levu Island, Fiji, 13 February 1974. Photograph: B. Carlson.

Figure 24. *H. carlsoni.* Length 48 mm. From 18 m, Nukubuco (=Sandbank) Channel, Main Suva Reef, Laucala Bay, Suva, Viti Levu Island, Fiji, 20 November 1987. Photograph: J. Brodie.

Explanation of Figures 25 to 32

Radula of *Halgerda aurantiomaculata.*

Figure 25. SEM of innermost lateral teeth of Fijian specimen; note elongate area of attachment to basal plate and flange on inner margin of blade. Bar = 0.05 μm.

Figure 26. SEM of middle lateral teeth from Fijian specimen. Bar = 0.1 μm.

Figure 27. SEM of outer edge of radula from Fijian specimen; note apical cleft on extreme outermost lateral teeth. Bar = 0.05 μm.

Figure 28. SEM of innermost lateral teeth of 55-mm Queensland specimen. Bar = 0.05 μm.

Figure 29. SEM of middle teeth from 55-mm Queensland specimen; note strong flange on inner proximal margin of blade. Bar = 0.1 μm.

Figure 30. SEM of outermost lateral teeth from 55-mm Queensland specimen; note apical cleft. Bar = 0.05 μm.

Figure 31. SEM of middle lateral teeth from 59-mm Queensland specimen. Bar = 0.1 μm.

Figure 32. SEM of outer edge of radula from 59-mm Queensland specimen; note absence of apical cleft on extreme outer lateral teeth. Bar = 0.05 μm.

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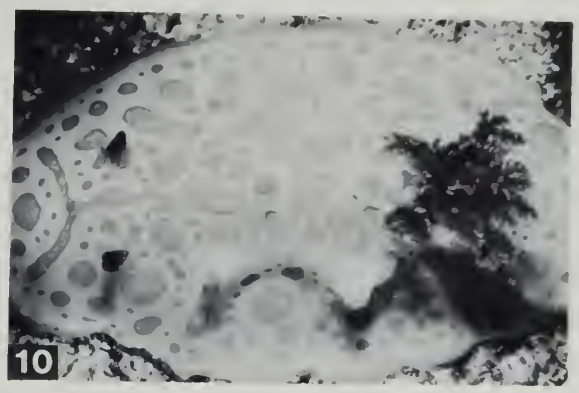
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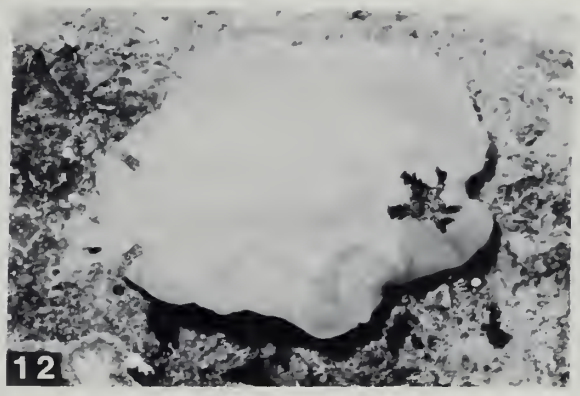
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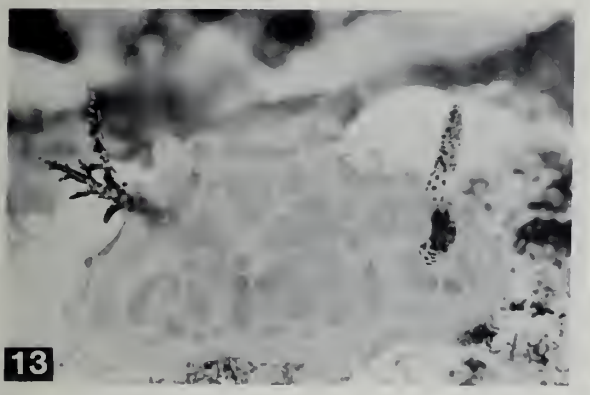
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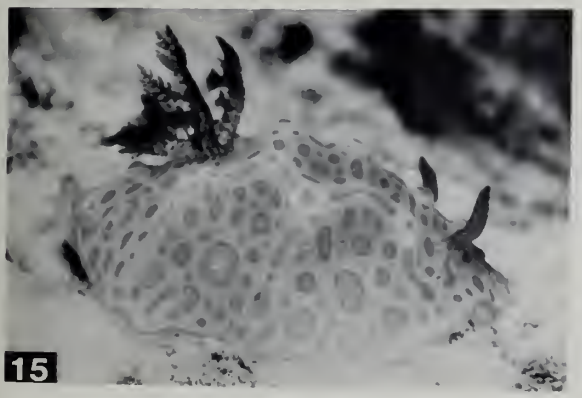
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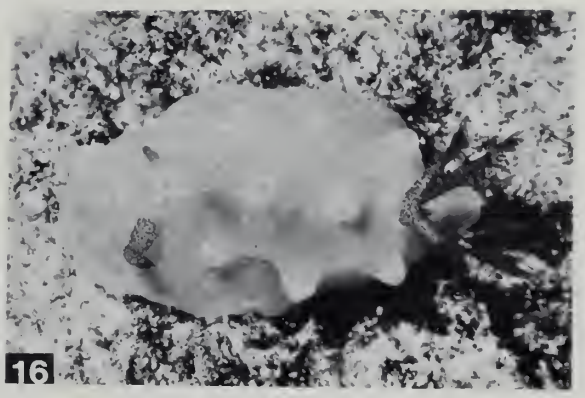
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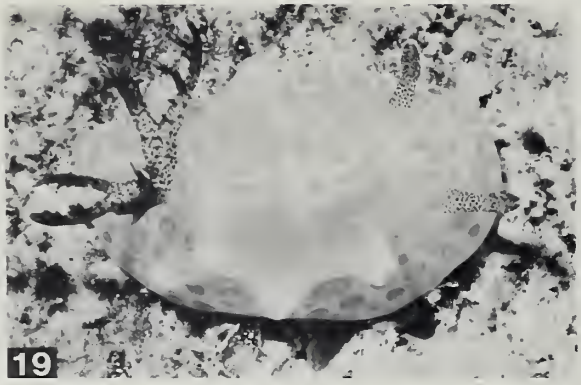
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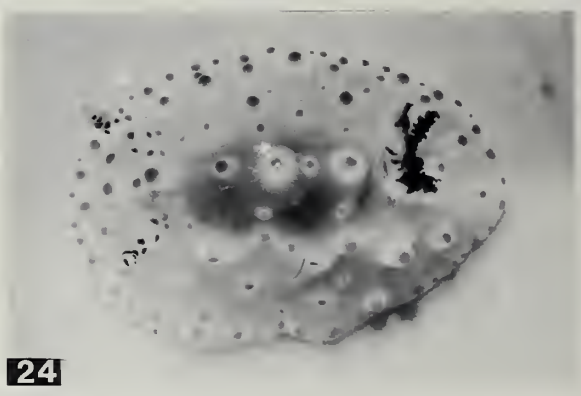
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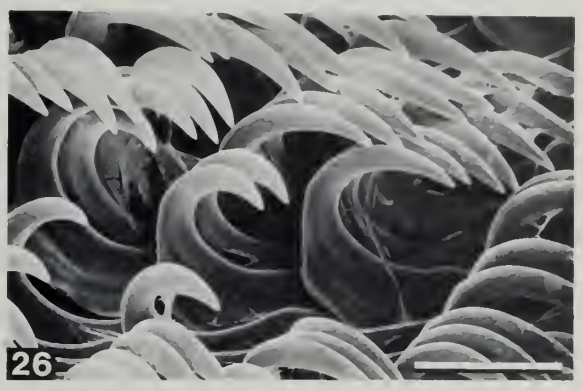
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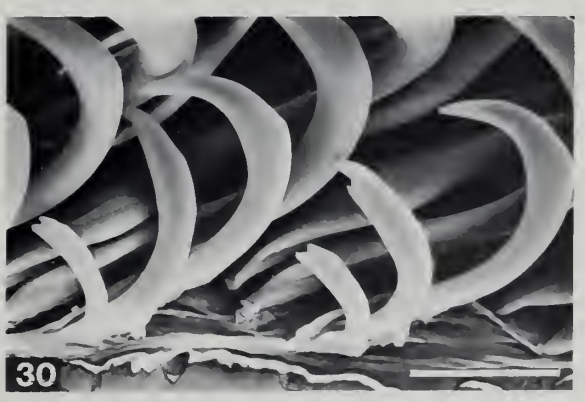
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vagina, *i.e.,* the longitudinal ridges and band of spots distally, and the lobulate glands medially. Nothing like this regional specialization has been reported previously for any other species of *Halgerda.*

By determining that the central region of the prostatic vas deferens completely ensheaths the bursa copulatrix in *Halgerda aurantiomaculata,* we have confirmed a generic character put forward by RUDMAN (1978:84) in his review of the genus *Halgerda.* This character would now appear to be the major internal autapomorphy for the entire genus. The other generic characters that this study has confirmed are those of mantle texture, sparsely pinnate gills, and elongate and curved radular sac. The tissue envelope that encases the viscera is very pale, translucent brown in *H. carlsoni* and *H. aurantiomaculata* (see above), contradicting the claim of it being very dark brown or black in species of *Halgerda.* Furthermore, these two species share relatively long, tapering rhinophores with a small clavus approximately equal in maximum diameter to the base of the stalk. RUDMAN (1978:83) indicated that all species of *Halgerda* possessed short, broad clavi. We doubt the color of the tissue envelope or proportions of the rhinophores are distinctive characters of the genus *Halgerda.*

GEOGRAPHICAL DISTRIBUTION

The Fijian specimens described above represent a range extension of approximately 2500 km eastwards. Previously, *Halgerda aurantiomaculata* had been recorded from throughout Queensland (coastal and Great Barrier Reef) and southeastern Papua New Guinean waters (WILLAN & COLEMAN, 1984). The southernmost record within this known range was a specimen collected by one of us (R.C.W.) at Flinders Reef, north of Cape Moreton in southern Queensland. Confirmation of this nudibranch's presence even further south, in the southern Coral Sea, comes by way of specimens from Elizabeth Reef and Lord Howe Island, one animal from each location.

Extensive field work along the northern New South Wales coastline (by experienced divers based at Coffs Harbour) and in the Madang Province on the northern coast of Papua New Guinea (by R.C.W. and T. M. Gosliner) have failed to reveal *Halgerda aurantiomaculata,* so we have reason to conclude its northern and southern limits coincide with those of the Coral Sea. We cannot presently explain its apparent absence in New Caledonia or Vanuatu, both island nations whose waters lie between northeastern Australia and Fiji.

ACKNOWLEDGMENTS

Neville Coleman willingly provided locality data for the Queensland, Papua New Guinea, and Lord Howe Island specimens of *Halgerda aurantiomaculata.* Ian Loch and Bill Rudman arranged the loan of material from The Australian Museum and Robert Burn did likewise from the Museum of Victoria. Bruce Carlson generously duplicated his slide of a paratype of *H. carlsoni* so we could include it here. We thank the following friends for allowing us to reproduce their original photographs in this paper: Jon Brodie, David Brunckhorst, Carol Buchanan, Neville Coleman, John Paterson, and Kathy Tubbenhauer. The scanning electron micrographs were taken by John Hardy of the University of Queensland's Electron Microscope Center. The manuscript was critically read by Jon Brodie, Robert Burn, and Clay Carlson, and we are grateful for their suggestions. R.C.W. acknowledges the Bureau of Flora and Fauna, Canberra, for financial support on his Great Barrier Reef sampling visits. Field work in Papua New Guinea was conducted from the Christensen Research Institute, Madang, with the tenure of a C.S.I.R.O. (Australia) fellowship.

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Bathydoris clavigera Thiele, 1912: Redescription of the Undissected Holotype, and the Synonymy of *B. obliquata* Odhner, 1934

by

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Abstract. The external morphology and anatomy of the hitherto undissected holotype of *Bathydoris clavigera* Thiele, 1912, are described. A comparison with the type material of *B. obliquata* Odhner, 1934, shows that the latter species is synonymous with *B. clavigera.*

INTRODUCTION

Thiele (1912) described a specimen of the genus *Bathydoris* which is similar to *B. hodgsoni* Eliot, 1907. According to Eliot (1907), the latter could be distinguished from *B. clavigera* by the smaller dorsal papillae and the position of the gills. Because of the great similarity of these two species of *Bathydoris,* Thiele decided not to dissect the only specimen of his new species. This led to the fact that recently found specimens have never been discussed in connection with *B. clavigera,* only with *B. obliquata,* a species described much more thoroughly by Odhner (1934). An examination of the anatomy of the holotype of *B. clavigera,* therefore, is essential for a revision of the genus *Bathydoris* and for the classification of the newly found bathydorids (Wägele, in preparation). Unfortunately a complete anatomical investigation was impossible because of the gelatinous consistency of the viscera, owing to poor preservation.

MATERIAL

Holotype of *Bathydoris clavigera*: Zoologisches Museum Berlin. Holotype and one paratype of *B. obliquata*: British Museum (National History) London, No. 1934.10.5.75.

EXAMINATION OF *Bathydoris clavigera* HOLOTYPE

External morphology: According to Thiele (1912) the length of the living animal was 90 mm and the breadth 50 mm. The preserved animal is 55 mm long and 26 mm broad, and has a gelatinous consistency. Since Thiele figured only the lateral view of the body, the dorsal view of the external form of the dark grayish-brown animal is represented in Figure 1A. The rhinophores are rather long and thick.

There is a gill plume on the right side of the mediodorsal anal papilla, consisting of three tripinnate gills, which are almost entirely detached from the notum.

The genital papilla has two distinct openings. The male opening lies on a small papilla, and the oviducal opening is covered by a tongue-like process (Thiele 1912:pl. 19, fig. 2).

Digestive tract: The oral tube is short and terminates at the labial disc, the protruded entrance to the strong pharynx. The thin cuticle of the labial disc, which is connected to the jaws, has a hairy appearance on the outer side. The straight masticatory edges of the light brown jaws are dark brown and connected with each other by membranes (Figure 1E, arrow). The radula (9 × 7 mm) has the formula: 35 × 50·1·1·1·50. The teeth are brown, whereas the membrane of the radula is yellow. The median tooth is broad and has no pronounced lateral cusps (Figure 1F). The cutting edge is very thin and irregularly serrate. The first laterals are broad, the following ones narrower. The length of their cusps increases in the following six teeth and decreases in the last five to 10 laterals. The cusps are very long compared to the tooth base (Figures 1F, G). The 38th lateral on the right side has a bifid cusp with an additional denticle (Figure 1H). The first laterals have a small denticle (Figure 1F) and several irregular serrations.

The large salivary glands cover most parts of the anterior esophagus (Figure 1B). They open into the latter by small ducts, which are dilated into ampullae at their proximal ends. The esophagus arises posterodorsally from the

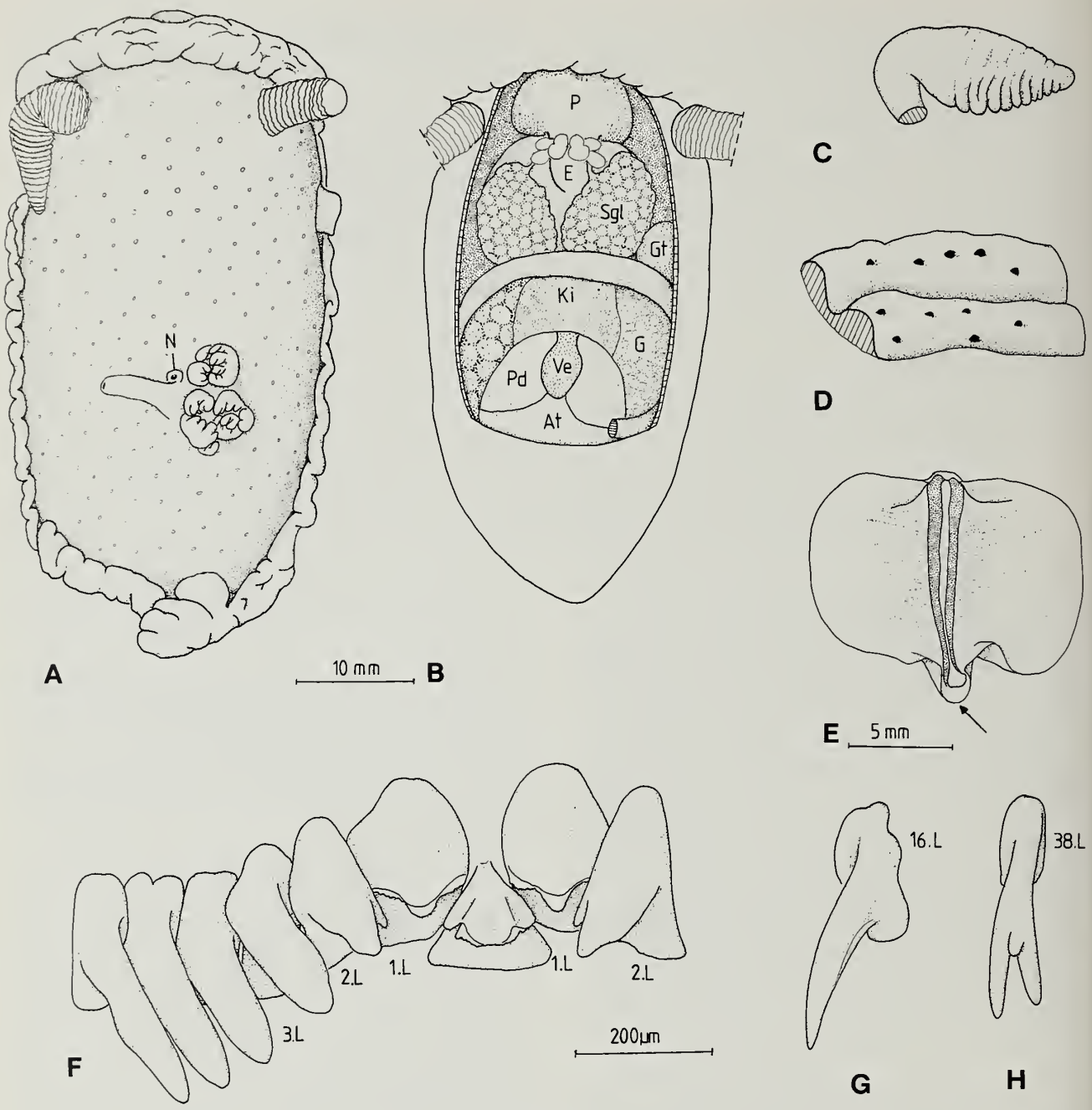

Figure 1

Bathydoris clavigera, holotype. A. External features. B. Organs in situ. C. Penis. D. Two folds of the posterior part of the esophagus with cuticularized cones. E. Jaws, still connected by membranes (arrow). F. Teeth from center of 10th row. G. Lateral, 5th row. H. Lateral with anomaly, 5th row. Key: At, atrium; E, esophagus; G, gonad; Gt, genital tract; Ki, kidney; N, nephroproct; P, pharynx; Pd, pericardium; Sgl, salivary gland; Ve, ventricle.

pharynx as a thin duct, leads to the right side, then distends into a sac-like structure. This anterior part of the esophagus is lined by longitudinal folds, which are masked by many smaller transverse folds. These folds are covered by a thin, light-brown cuticle. The transition into the posterior part of the esophagus lies ventral to the digestive gland. This part only shows longitudinal folds with knoblike structures or cones (Figure 1D).

The transition from stomach to intestine and the presence of a caecum could not be examined. The intestine traverses the viscera from the left to the right side and opens posteriorly at the anal papilla.

Nervous system: The cerebral ganglia of the poorly preserved nervous system are round and a division into halves by a notch is hardly visible. The rhinophoral ganglia are situated medially on the cerebral ganglia. The distinct pleural and pedal ganglia are connected with the cerebral ganglia by short, hardly visible connectives. Three subesophageal commissures of equal length could be identified (pedal and parapedal commissure, visceral loop). The large buccal ganglia are widely separated from each other. Gastro-esophageal ganglia could not be identified. Because of the loss of pigment, the eyes were found only after a careful examination at the base of the rhinophores.

Genital system: The genital system is in a very poor condition. Therefore, dissection has not been attempted, except for the penis, which has an elongate, flattened, slightly conical shape. Its surface is more or less smooth and shows folds only on one side (Figure 1C).

Further organ systems: There is no blood gland or a gland in the atrium. The heart lies more or less symmetrically on the viscera (Figure 1B).

DISCUSSION

Up to now 11 species of *Bathydoris* have been described, six of them from Antarctic waters: *B. clavigera, B. hodgsoni* Eliot, 1907, *B. inflata* Eliot, 1907, *B. brownii* Evans, 1914, *B. obliquata* Odhner, 1934, and *B. vitjazi* Minichev, 1969. Only *B. obliquata* shows a radula similar to that of *B. clavigera*: the first lateral is clearly distinct in size and shape from the other laterals. According to the descriptions of Odhner (1934) and the results of a re-examination of the holotype of *B. obliquata,* the external morphology (*e.g.*, length of rhinophores) and the anatomy (hairy appearance of lip cuticle, shape of radula and teeth, existence of eyes) are virtually identical. *Bathydoris obliquata* differs from *B. clavigera* only in the position of a second gill in front of the anus. Because of the poor condition of the notum in the specimen of *B. clavigera,* the presence of a second gill in front of the anus cannot be discounted. According to this study and the results on fresh material from the Weddell Sea (Wägele, unpublished data) it can be concluded that these two species are synonymous in spite of the differences in their gills.

ACKNOWLEDGMENTS

I thank Prof. Dr. L. Schmekel (Münster) and Prof. Dr. H.-K. Schminke (Oldenburg) for their help during the preparation of this study. Dr. Kilias (Berlin) and Dr. Evans (London) kindly sent me the type material. This study was supported by the Deutsche Forschungsgemeinschaft and by funds of the Minister für Wissenschaft und Kunst, Niedersachsen.

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Four Additional Species of *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from Sonora, Mexico

by

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Abstract. Four new species of *Sonorella* from north-central and northeast Sonora, Mexico, are described, illustrated, and compared to the following related species: *S. magdalenensis* (Stearns, 1890), *S. fransciscana* Pilsbry & Ferriss, 1919, *S. baboquivariensis depressa* Pilsbry & Ferriss, 1915, *S. mormonum mormonum* Pilsbry, 1948, *S. m. huasabasensis* Miller, 1967, and *S. perhirsuta* Miller, 1967. Two of them are from the Chihuahuan Desertscrub, another from the Madrean Evergreen Woodland, and the other from the Semidesert Grassland bioregions.

INTRODUCTION

Miller (1967b, c) added four new records to the poorly known snail fauna of Sonora (only four species of *Sonorella* were known at the time). He suggested that the southern limit of the genus *Sonorella* in central Sonora was determined by the locality of *Sonorella perhirsuta* Miller, 1967. Later, Bequaert & Miller (1973) listed the eight species found in Sonora by that time, and drew the limits of the distribution of the genus in the southwest United States and northwest Mexico. Much of northern Sonora still remained to be explored, and from 1973 to date six new species have been described (Naranjo & Miller, 1986; Naranjo, 1988a, b). Continued exploration has resulted in the discovery of the four new species described below.

The following abbreviations are used: SBMNH, Santa Barbara Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution; ANSP, Academy of Natural Sciences of Philadelphia; FMNH, Field Museum of Natural History; UTEP, University of Texas at El Paso; UNAM, Universidad Nacional Autonoma de Mexico Coleccion Malacologica; ENG, E. Naranjo-Garcia, and WBM, W. B. Miller.

METHODS

The reproductive systems were dissected out and preserved as whole mounts in accordance with the method of Gregg (1959; Miller, 1967a, and Miller, personal communication) as follows. The specimen to be mounted consists of the dissected reproductive system of the snail, which is attached to the base of a cork by means of a short, bent insect pin through a flap of tissue at the genital orifice. The specimen is immersed in a vial filled with haematoxylin (saturated solution), suspended from the cork, which is used to stopper the vial, for a period of about 9 min. It is then removed and immersed in a similar-sized vial filled with destaining solution (2% HCl in 70% ethanol) for 2–5 min, until the specimen has changed color from deep black to light purple. It is removed and placed in 70% ethanol for a period of 3–5 min, sufficient to dilute most of the absorbed acid. Finally it is placed in an eosin stain (saturated solution of eosin-Y in 70% ethanol), where it may remain indefinitely, until it can be mounted. Protracted immersion in the eosin solution, however, will cause hardening of the tissues prior to mounting. Normally, 1–2 min of immersion are adequate for eosin staining.

The specimen is removed from the eosin solution and placed on a slide (25 × 75 mm or 50 × 75 mm for large specimens). At this time, the structures can be cleaned of bits of attached connective tissue, and the organs separated and straightened (for subsequent measurements and comparative examination). A cover slip, or a similar slide, to which a very fine film of vaseline has been applied on the underside, is then placed on top of the specimen, and the slide, mount, and cover slip are tied firmly together with a piece of thread near each end to prevent the specimen from falling out during the dehydration and clearing processes. The vaseline is used to prevent sticking of the cover

Figure 1

A. *Sonorella* ***torreonica*** Naranjo-Garcia, sp. nov. Shell of paratypes and holotype (middle), SBMNH 34951. Umbilicus; aperture; apical view. B. *Sonorella* ***sasabe*** Naranjo-Garcia, sp. nov. Shell of paratypes and holotype (middle), SBMNH 34954. Umbilicus; aperture, apical view.

slip to the specimen when it is removed for embedding in Permount® (histological mounting medium from Fisher Scientific).

The whole mount is dehydrated in a series of three jars of 100% ethanol. Since the dissection is usually done under 70% ethanol, the mount can be placed directly into 100% ethanol. The whole mount is immersed in each jar for a minimum of one day. This assures maximum removal of water from the tissues.

After the third immersion in 100% ethanol the whole mount is transferred to a jar filled with 50% toluene and 50% ethanol, where it is kept for a minimum of one day. It is then immersed in a series of four toluene-filled jars, a minimum of one day per jar, in order to assure that all of the ethanol has been removed from the tissues. This process also serves to clear the lipids from the tissues and allows the transparent viewing of internal structures.

After the fourth toluene immersion, the whole mount is placed on a flat surface, the cover slip is removed, and a layer of Permount is poured over the preparation. A clean cover slip, or slide, is placed on top, and care is taken to eliminate bubbles. The whole mount is then set aside to dry. The drying process may take several days and additional Permount may need to be added, with a pipette, to compensate for evaporation during the drying process.

Permanent mounts are stored horizontally in covered, dust-free containers.

DESCRIPTIONS

Family Helminthoglyptidae Pilsbry, 1939

Genus *Sonorella* Pilsbry, 1939

Sonorella ***torreonica*** Naranjo-Garcia, sp. nov.

(Figures 1A, 2)

Description of shell of holotype (Figure 1A): Shell globose, heliciform, light tan, with dark brown spiral band

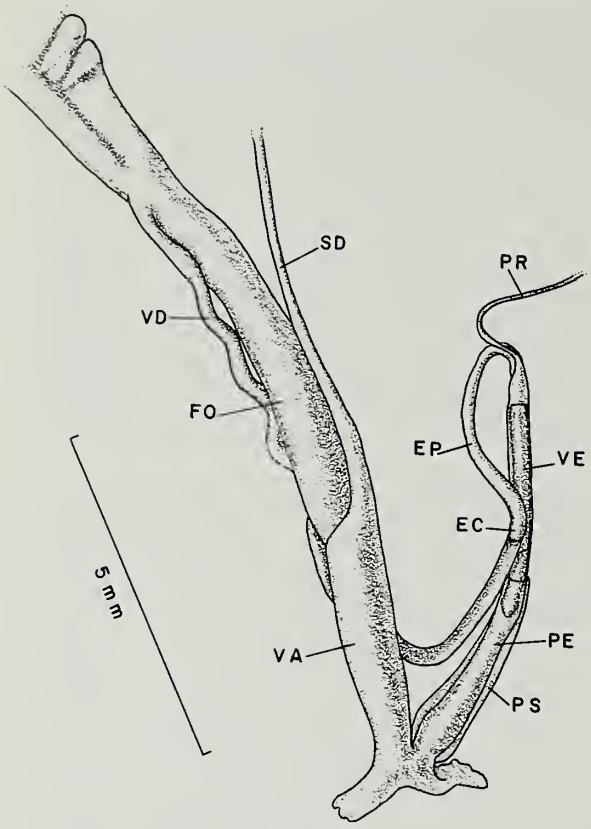

Figure 2

Sonorella ***torreonica*** sp. nov. Lower reproductive anatomy of holotype, SBMNH 34951. EC, epiphallic caecum; EP, epiphallus; FO, free oviduct; PE, penis; PR, retractor muscle; PS, penial sheath; SD, spermathecal duct; VA, vagina; VD, vas deferens; VE, verge.

on rounded shoulder. Narrowly umbilicate, umbilicus contained 10 times in diameter of shell, ¼ covered by reflected columellar lip. Embryonic shell of about 1½ whorls. Apex with heavy wrinkles followed by spiral descending and ascending threads, and granules superimposed on finer wrinkles. Post-apical whorls with growth wrinkles and occasional weak punctae and granules. Body whorl somewhat silky in appearance, and with radial growth wrinkles descending just behind aperture. Aperture oblique, ovate-lunate, margins converging. Parietal callus thin. Lip slightly thicker than rest of shell. Shell measurements in mm: diameter 18.0; height 11.9; umbilicus 1.8; whorls 4.

Reproductive system (Figure 2): Apical structures characteristic of genus. Penis short, slender, increasing in diameter at junction with vagina, inner walls faintly glandular. Verge smooth, about ½ length of penis, with conical tip. Penial sheath about ½ length of penis. Lumen of epiphallus rather wide; inner walls glandular. Epiphallic caecum minuscule. Vagina stout, slightly shorter than penis; inner walls smooth. Measurements in mm: penis 5.2; verge 3.0; penial sheath 2.7; vagina 3.2; epiphallic caecum 0.4.

Type locality: Mexico, Sonora, Sierra el Torreón, 17 road miles (27 km) SE Magdalena on road to Cucurpe; 30°27.8'N, 110°48.5'W; elevation ca. 1050 m, under volcanic rocks.

Type material: Holotype: SBMNH 34951 (shell and dissected soft anatomy).

Paratypes: USNM 859326; ANSP 370245; FMNH 205938; UTEP 11105; UNAM 1211; ENG 469 and 535; WBM 7454 and 7512.

Etymology: This species is named after the mountain range in which it lives, Sierra el Torreón.

Remarks: The habitat corresponds to the Madrean Evergreen Woodland biotic community of Brown (1982). Primary vegetation includes: *Cassia leptocarpa, Ceanothus huichugore, Cupressus arizonica, Dodonea viscosa, Erythrina flabelliformis, Garrya wrightii, Juniperus deppeana, J. monosperma, Mimosa biuncifera, Quercus oblongifolia, Rhamnus betulaefolia, Rhus choriophylla, Rhus trilobata,* and *Tillandsia recurvata.*

Sonorella ***sasabe*** Naranjo-Garcia, sp. nov.

(Figures 1B, 3)

Description of shell of holotype (Figure 1B): Shell depressed-globose, heliciform, thin, glossy, light brown with a darker reddish-brown band on upper region of rounded shoulder. Umbilicus contained 7.7 times in diameter of shell. Embryonic shell of one whorl; apex of embryonic shell smooth with fine radial ripples, followed by fine reticulate sculpture, subsequently fine but strong descending striae on top of growth wrinkles. Sculpture almost disappears, on post-apical whorls only growth wrinkles and scattered, very fine rounded papillae remain. Body whorl only with growth wrinkles. Aperture ovate-lunate, wider than high, lips converging and basal lip slightly covering umbilicus. Shell measurements in mm: diameter 17.8; height 10.5; umbilicus 2.3; whorls 4.

Reproductive anatomy (Figure 3): Penis long, glandular, upper ⅓ containing stout, almost cylindrical verge; verge thickening from apical region to center, sculptured with diagonal furrows not interconnected, conical tip; seminal duct terminal. Epiphallus about same length as penis, bearing small epiphallic caecum embedded in connective tissue. Penial sheath ca. ⅓ length of penis. Vagina slightly longer than penis, inner wall glandular, cylindrical, slender at basal end, with very prominent and strong muscular collar on upper portion near apical end. Free oviduct glandular. Measurements in mm: penis 10.9; verge 4.4; penial sheath 3.5; vagina 11.9; free oviduct 3.2; epiphallus 11.0.

Type locality: Mexico, Sonora, Sierra Pozo Verde, on E flank of Cerro El Sasabe, 4 km S of Sasabe on road to

Altar; 31°26.3'N, 111°33.8'W; elevation ca. 1050 m in igneous boulders.

Type material: Holotype: SBMNH 34954 (shell and dissected soft anatomy).

Paratypes: USNM 859325; ANSP 370244; FMNH 205939; UTEP 11104; UNAM 1212; ENG 473; WBM 7243 and 7447.

Etymology: This species is named after the nearby mountain (Cerro El Sasabe) and town, El Sasabe.

Remarks: The habitat corresponds to the Semidesert Grassland biotic community of BROWN (1982). The main vegetation includes: *Prosopis glandulosa, Acacia greggii, Fouquieria splendens, Carnegiea gigantea, Larrea tridentata,* and *Opuntia phaeacantha.*

Sonorella ***madreana*** Naranjo-Garcia, sp. nov.

(Figures 4A, 5)

Description of shell of holotype (Figure 4A): Shell depressed-globose, heliciform, thin, silky, light brown with narrow, chestnut spiral band on upper shoulder; shoulder rounded. Umbilicus narrow, approximately ⅛ diameter of shell, slightly covered by reflected columellar lip. Embryonic shell of about 1½ whorls, with radial ripples, rounded granules on ascending and descending threads, and roughened appearance; abruptly changing to rounded granules on strong radial wrinkles. Post-embryonic whorls with growth wrinkles. Aperture oblique, rounded, margins converging, peristome delicately expanded. Shell measurements in mm: diameter 17.8; height 10.9; umbilicus 2.3; whorls 4½.

Reproductive system (Figure 5): Penis long, ⅔ of upper inner walls glandular, containing long, smooth cylindrical verge, barely tapering to tip; seminal duct opening subterminally adjacent to diagonally pointed tip; verge about ½ length of penis. Penial sheath enveloping about ½ of penis. Epiphallus thin with detached, rather short epiphallic caecum. Vagina barely shorter than penis, wider at apical end, inner walls glandular. Measurements in mm: penis 9.4; verge 4.9; penial sheath 4.5; epiphallic caecum 1; vagina 7.1.

Type locality: MEXICO, Sonora, Sierra Las Minitas, ca. 2 km SE of Rancho Jucaral buildings; 31°11.1'N, 109°4.7'W; elevation ca. 1400 m, in rhyolite rockslide.

Additional locality: MEXICO, Sonora, Sierra Las Minitas, along east bank of Rio Los Embudos, in rockpile ca. ½ km E of Rancho El Jucaral buildings; 31°11.8'N, 109°5.2'W; elevation ca. 1200 m.

Type material: Holotype: SBMNH 34952 (shell and dissected soft anatomy).

Paratypes: USNM 859327; ANSP 370243; FMNH 205936; UTEP 11103; UNAM 1214; ENG 403; WBM 7407.

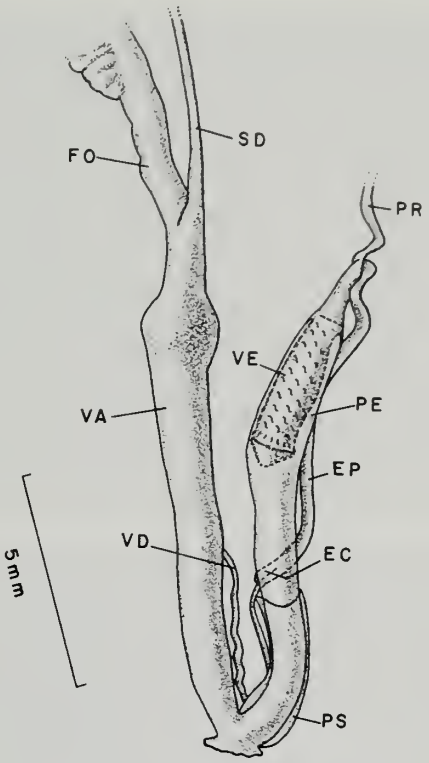

Figure 3

Sonorella ***sasabe*** sp. nov. Lower reproductive anatomy of holotype, SBMNH 34954. EC, epiphalic caecum; EP, epiphallus; FO, free oviduct; PE, penis; PR, penial retractor muscle; PS, penial sheath; SD, spermathecal duct; VA, vagina; VD, vas deferens; VE, verge.

Etymology: This species is named after the Sierra Madre Occidental, in which the Sierra Las Minitas is an outlier.

Sonorella ***walteri*** Naranjo-Garcia, sp. nov.

(Figures 4B, 6)

Description of shell of holotype (Figure 4B): Shell depressed-globose, heliciform, thin, shiny, tan, with darker brown spiral band on well rounded shoulder. Umbilicus rather wide contained about 6 times in diameter. Embryonic shell of about one whorl, with small smooth area on apex, followed by rounded granules on closely spaced radial wrinkles, and extremely subtle spiral descending striae on upper surface (worn smooth in live specimens); sculpture stronger near suture; succeeding whorls with granules on growth wrinkles, granules gradually disappearing to body whorl leaving only wrinkles. Body whorl descending steeply to scarcely expanded peristome. Aperture oblique, rounded, wider than high, margins converging, parietal callus thin. Measurements in mm: diameter 20.0; height 11.9; umbilicus 3.3; whorls 5.

Reproductive system (Figure 6): Penis long, enveloped by penial sheath for approximately ¼–⅓ of its length.

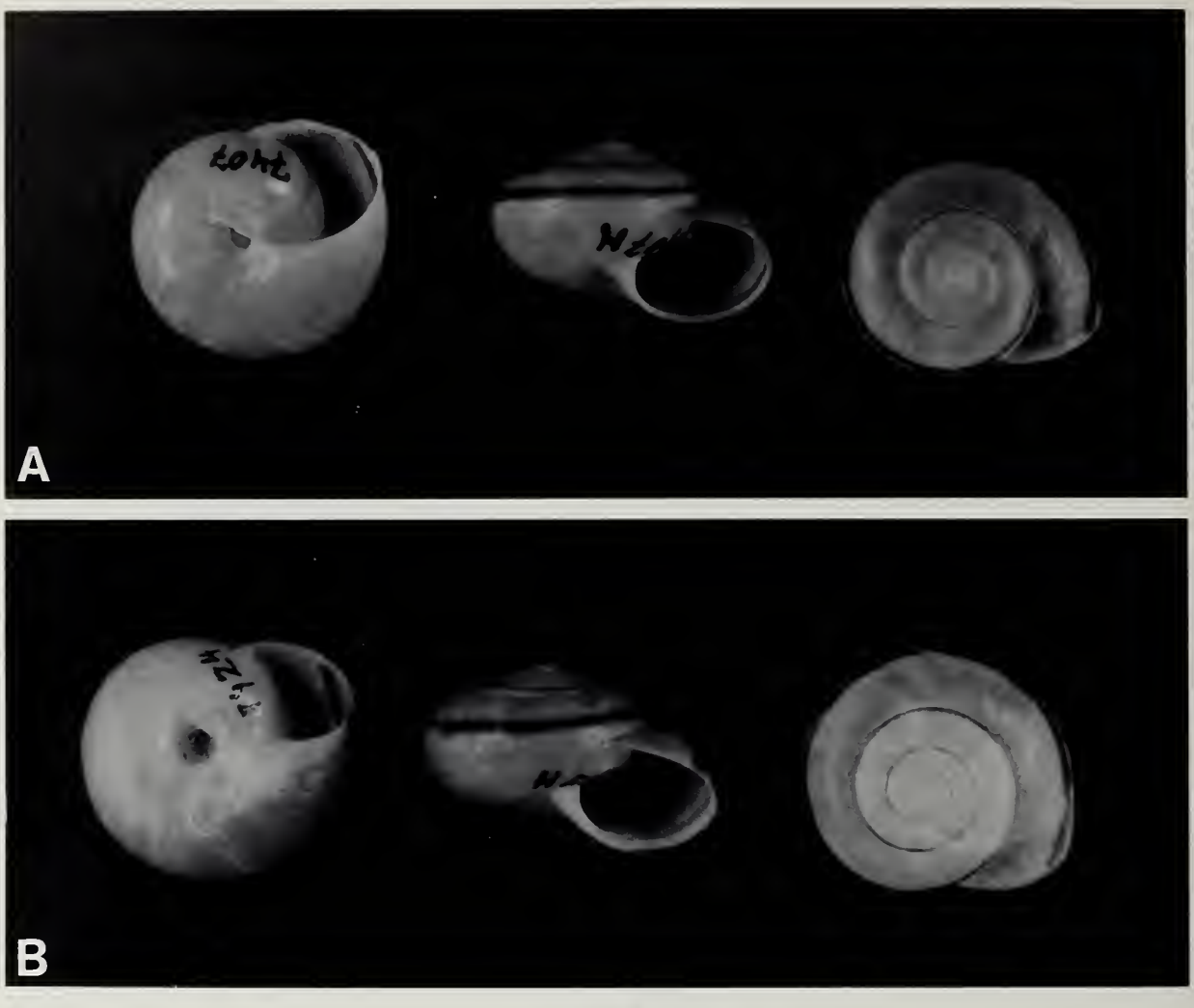

Figure 4

A. *Sonorella* ***madreana*** Naranjo-Garcia, sp. nov. Shell of paratypes and holotype (middle), SBMNH 34952. Umbilicus; aperture; apical view. B. *Sonorella* ***walteri*** Naranjo-Garcia, sp. nov. Shell of paratypes and holotype (middle), SBMNH 34953. Umbilicus; aperture; apical view.

Verge long, cylindrical, smooth, with fine undulations, with central seminal duct and acute tip. Epiphallus shorter than penis, bearing distinct epiphallic caecum surrounded by connective tissue. Vagina longer than penis, cylindrical. Free oviduct almost ½ length of vagina. Measurements in mm: penis 8.4; verge 3.6; penial sheath 2.8; epiphallus 5.6; epiphallic caecum 1.9; vagina 10.0; free oviduct 4.5.

Type locality: MEXICO, Sonora, Cerro Gallardo, ca. 1.5 km S of Rancho Gallardo buildings; 31°17.8′N, 109°23.4′W; elevation ca. 1500 m; in N facing rhyolite rockpiles below cliffs.

Type material: Holotype: SBMNH 34953 (shell and dissected soft anatomy).

Paratypes: USNM 859324; ANSP 370246; FMNH 205937; UTEP 11106; UNAM 1213; ENG 537; WBM 7424.

Etymology: This species is named for Walter B. Miller, who has greatly contributed to the knowledge of the land snail fauna of the Southwest.

Remarks: The latter two species described are found in the Chihuahuan Desertscrub biotic community of BROWN (1982), which is defined by the following plants: *Larrea tridentata, Prosopis glandulosa* var. *torreyana, Acacia greggii, Coldenia canescens, Dasylirion leiophyllum, Fouquieria splendens, Jatropha dioica, Juniperus monosperma, Krameria parvifolia* var. *glandulosa,* and *Rhus microphylla.*

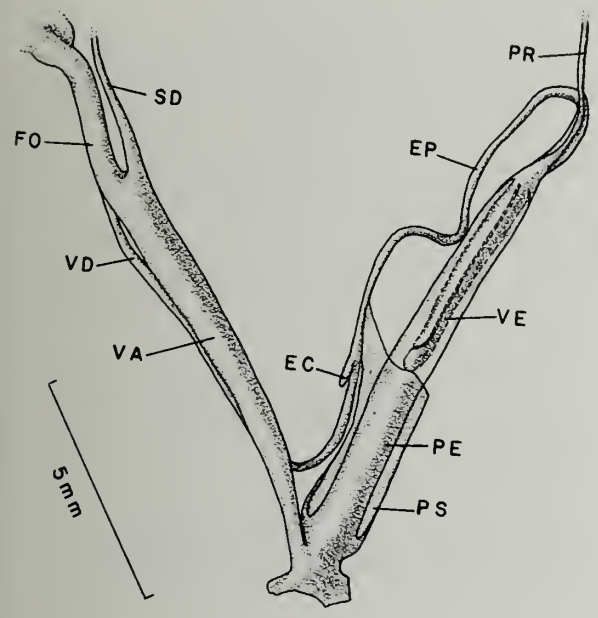

Figure 5

Sonorella ***madreana*** sp. nov. Lower reproductive anatomy of holotype, SBMNH 34952. EC, epiphallic caecum; EP, epiphallus; FO, free oviduct; PE, penis; PR, penial retractor muscle; PS, penial sheath; SD, spermathecal duct; VA, vagina; VD, vas deferens; VE, verge.

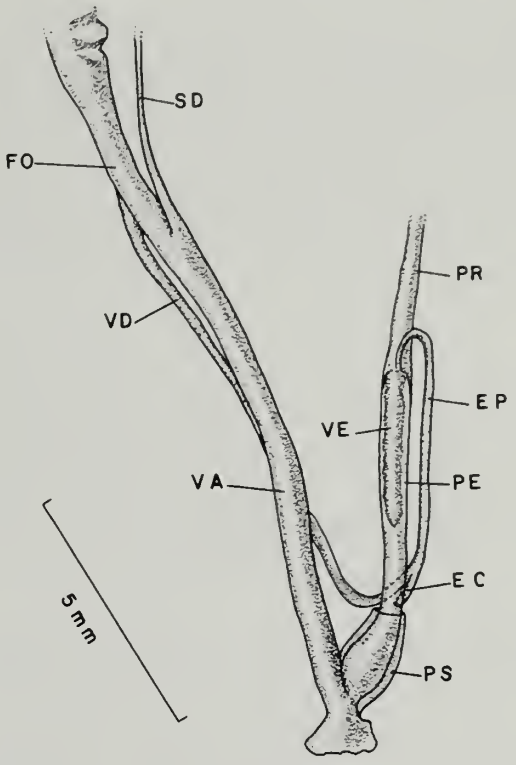

Figure 6

Sonorella ***walteri*** sp. nov. Lower reproductive anatomy of holotype, SBMNH 34953. EC, epiphallic caecum; EP, epiphallus; FO, free oviduct; PE, penis; PR, penial retractor muscle; PS, penial sheath; SD, spermathecal duct; VA, vagina; VD, vas deferens; VE, verge.

DISCUSSION

Sonorella ***torreonica*** appears to be related to *S. mormonum mormonum* Pilsbry, 1948, and *S. mormonum huasabasensis* Miller, 1967, because these three taxa share short and slender basal reproductive structures. *Sonorella* ***torreonica*** differs by having a shorter vagina and penis and by lacking the glandular inner walls present in the two *S. mormonum* subspecies. The verge in *S. m. mormomum* is thicker and rounded at the tip, and has a depressed conical dimple, whereas in *S.* ***torreonica*** the verge is cylindrical, slender, and has a conical, pointed tip. In *S. m. huasabasensis* the verge is rather cylindrical, somewhat thicker at mid length and tapering finely to a blunt tip. In addition in both *S. mormonum* subspecies the verge is ⅓ to almost ½ the length of the penis, whereas in *S.* ***torreonica*** the verge is ⅔ this length. In *S.* ***torreonica*** and *S. m. huasabasensis* the vagina is about the length of the penis, whereas in *S. m. mormonum* the penis is longer than the vagina.

Sonorella ***sasabe*** resembles *S. magdalenensis* (Stearns, 1890). However, they differ in the fat, blunt verge of *S.* ***sasabe*** and the longer vagina and free oviduct of *S. magdalenensis*. The vagina is about ⅓ longer than the penis in *S. magdalenensis,* while in *S.* ***sasabe*** they are about the same length. Additionally, *S.* ***sasabe*** possesses a strong vaginal collar located in the vicinity of the apical end of the vagina, while in *S. magdalenensis* the vaginal collar is much smaller and located about halfway along the length of the vagina.

Sonorella ***madreana*** resembles *S. perhirsuta* Miller, 1967, but strong differences separate these species, the main one being the persistently hairy shell of *S. perhirsuta.* In both species the length of the vagina and the penis are approximately the same. In *S.* ***madreana*** the seminal duct opening is consistently subterminal, opening in proximity to the basal end of the verge, whereas in *S. perhirsuta* it opens more apically about ⅔–¾ of the way along the length of the verge (Miller, 1967b). The verge in both species is long and full, with a blunt diagonal tip, although less defined in *S. perhirsuta. Sonorella perhirsuta* has an ample cylindrical vagina along its entire length, whereas *S.* ***madreana*** has a slender cylinder diminishing in diameter to the gonopore.

The reproductive anatomy of *Sonorella* ***walteri*** is somewhat similar to that of *S. franciscana* Pilsbry & Ferriss, 1919, and *S. baboquivariensis depressa* Pilsbry & Ferriss, 1915. Differences exist, however, in specific measurements of the principal structures as follows: the verge has a blunt tip and is greater than ½ the length of the penis in *S.*

franciscana; in *S. **walteri*** the verge has an acute tip and is shorter than ½ the length of the penis; the verge has a blunt tip and is only ⅓ the length of the penis in *S. b. depressa*. The penis is ½ the length of the vagina in *S. franciscana*, ⅔ the length of the vagina in *S. **walteri***, and equal to the length of the vagina in *S. b. depressa*. In view of the fact that *S. **walteri*** is geographically separated from both *S. franciscana* and *S. b. depressa* by over 240 km, with no intervening intergrading populations, these anatomical similarities are considered to result from convergence.

ACKNOWLEDGMENTS

I am indebted to Walter B. Miller for his advice, loan of material, and, together with James Hoffman, for their companionship in the field. Russell Davis, Ronnie Sidner, and George Ferguson have provided assistance in various ways. This research was supported by a doctoral grant from Consejo Nacional de Ciencia y Tecnologia.

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A New Species of *Holospira* (Gastropoda: Pulmonata) from Sonora, with the Reproductive Anatomy of *Holospira minima*

by

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Abstract. A new species, *Holospira* ***milleri*** Gilbertson, from the Rio Yaqui valley in eastern Sonora, Mexico, is described. The reproductive anatomy of another Sonoran species, *Holospira minima* von Martens, 1897, is illustrated and compared.

INTRODUCTION

The northwestern Mexican states of Sonora and Sinaloa are geographically isolated from the rest of the country by the Sierra Madre Occidental and the Gulf of California. Because of these barriers, this region is inhabited by a special group of *Holospira* species (PILSBRY, 1953:151–156). Present knowledge of these species is based almost entirely on shell characteristics, mostly from river drift specimens; their reproductive anatomies have remained unknown. The majority (5 of 7) are members of the endemic subgenus *Allocoryphe* Pilsbry, 1946. The type species of *Allocoryphe* is *H. minima*.

Specimens of a new species described herein were first collected by Dr. Walter B. Miller of the University of Arizona along with his wife, Betty Sue, and graduate students Edna Naranjo-Garcia, Jane E. Deisler, and James E. Hoffman while on a field expedition to Sonora in November 1983. They remained unidentified until I initiated studies on the genus *Holospira* under Dr. Miller's sponsorship in 1987. Further field work in Sonora (and Sinaloa) should yield additional new species.

SYSTEMATICS

Family UROCOPTIDAE

Genus *Holospira* von Martens, 1860

Subgenus *Holospira s.s.* von Martens, 1860

Holospira ***milleri*** Gilbertson, sp. nov.

(Figures 1, 2)

Diagnosis: A moderately small *Holospira* with a tapered, quadrilamellate shell. The reproductive anatomy is characterized by the lack of a spermathecal diverticulum and by the presence of a verge in the penial complex.

Description of shell of holotype: Shell light brown, thin, somewhat translucent with periostracum remaining between the axial riblets, turret-shaped, and comprised of 13.2 whorls. Embryonic whorls 2.5 in number, rounded, smooth, very slightly tilted, and tapered toward apex. Postembryonic apical whorls 7 in number, strongly convex (subcarinate), also gradually tapered toward apex (not conic). Whorls of cylindric portion nearly 4 in number, not quite as convex, with greatest diameter above midline, and approximately equal in size. All postembryonic whorls evenly, thinly striated with oblique axial riblets bent slightly at angle of whorl. Riblets on penultimate whorl ca. one-third width of intercostal space and 62 in number. Umbilicus perforate, 0.5 mm in diameter. Aperture slightly ovate. Peristome expanded and slightly extended from body whorl. Armature of 4 strong lamellae located in last half of penultimate whorl with the large parietal (superior) and axial extending into first third of body whorl (Figure 1C). Maximum height 12.4 mm, diameter 3.5 mm.

Variations in paratypes: Eleven representative paratypes range from 10.8 to 12.5 mm (mean 11.8) in length, and from 3.5 to 3.8 mm (mean 3.6) in diameter. Whorls number from 10.5 to 12.5 (mean 11.9). Basal and palatal lamellae less distinct in some paratypes compared with holotype. Embryonic and early whorls straight (not slightly tilted) in paratypes.

Description of radula: Radula similar to other described radulae in genus. Radular formula typically 15·7·1·7·15. Central and lateral teeth with single conic mesocone. First marginal tooth characterized by development of small ectocone which gradually enlarges on ensuing marginals;

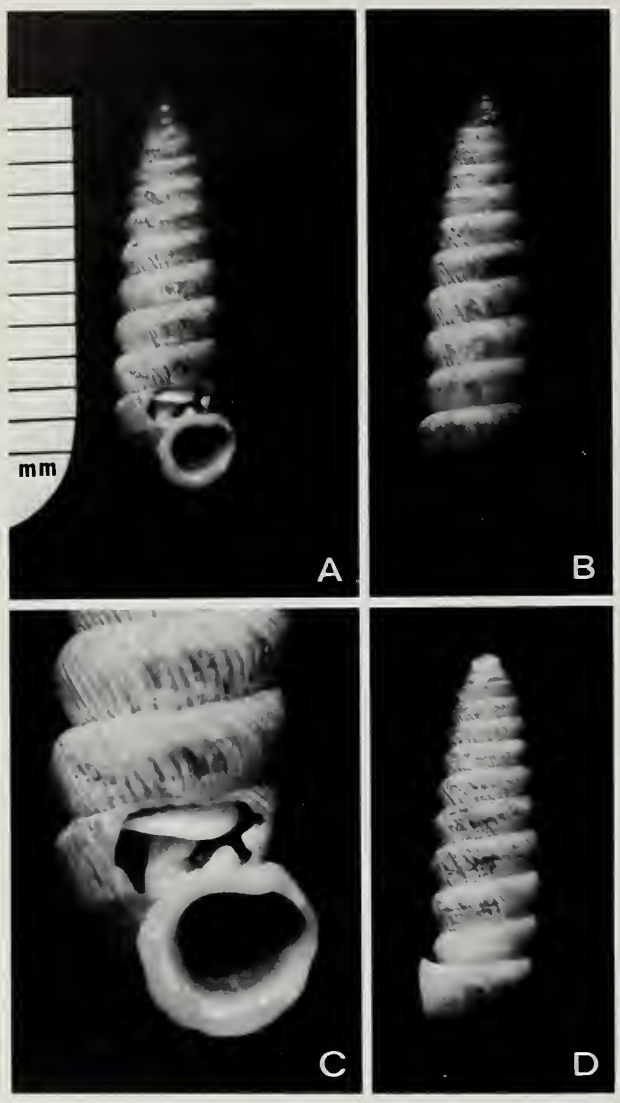

Figure 1

A, B, C. *Holospira* ***milleri*** Gilbertson, sp. nov., holotype, Santa Barbara Museum of Natural History No. 35042, apertural view, dorsal view, and enlargement to show lamellae. D. Side view of paratype.

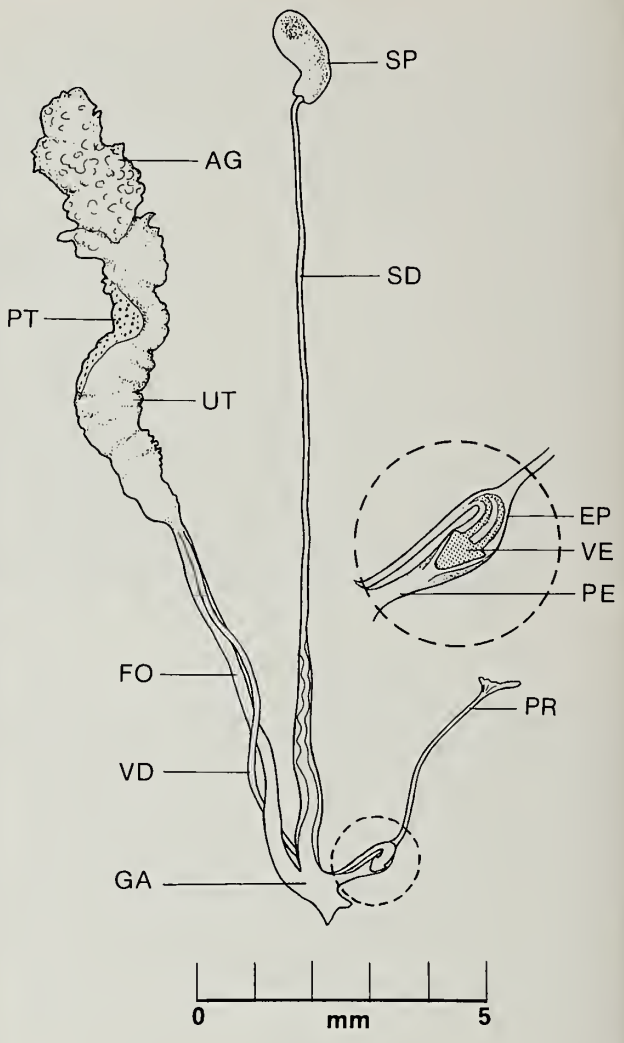

Figure 2

Reproductive system of *Holospira* ***milleri***. Specimen collected at the type locality by W. B. Miller, 27 Nov. 1983. Shell broken for dissection. AG, albumen gland; EP, epiphallus; FO, free oviduct; GA, genital atrium; PE, penis; PR, penial retractor muscle, PT, prostate gland; SD, spermathecal duct; SP, spermatheca; UT, uterus; VE, verge; VD, vas deferens.

mesocone becoming variably bifid on marginals ca. 7–14. Last marginal small and variable.

Description of reproductive anatomy: Description and measurements are of anatomy illustrated in Figure 2. Genital atrium connected to body wall by a short neck. Penis relatively small, expanding around a short, conical verge to summit of penial sac where it merges with epiphallus. Vas deferens descending along free oviduct, as usual, then proceeding upward along penis to epiphallus. Penial retractor muscle long and slender, inserting on apex of epiphallus. Spermathecal duct long, slender, lacking a diverticulum; basal portion widened, followed distally by a short section that is convoluted internally. Spermatheca comma-shaped and slightly invaginated where it receives spermathecal duct. Vagina lacking. Free oviduct slender and rather long. Uterus typically thickened and coiled with prostate gland imbedded in it. Albumen gland irregular in shape. Length measurements, in mm, of distinctive features as follows: penis, 0.8; spermathecal duct, 13.0; epiphallus, 0.4; spermatheca, 1.3; penial retractor, 3.2; free oviduct, 6.0.

Type locality: Sonora, Mexico: on the east side of the Rio Yaqui, under conglomerate rocks (containing calcite) in a ravine near the mouth of El Alamo wash, ca. 1.5 km south of the military footbridge at El Novillo; 28°58.1'N, 109°37.5'W; elevation ca. 260 m. This is within the Sinaloan thornscrub biome (BROWN, 1982). Dominant plants noted at the site include *Abutilon* sp., *Acacia cymbispina, Ceiba acuminata, Guaiacum coulteri, Lysiloma divaricata, Pachycereus pecten-aboriginum, Pithecellobium* sp., *Stenocereus thurberi,* and *Prosopis* sp. Access to the site is somewhat limited by the proximity of the Rio Yaqui and a nearby military installation.

Disposition of types: Holotype: Santa Barbara Museum of Natural History No. 35042. Paratypes: Academy of Natural Sciences of Philadelphia No. 371716; National Museum of Natural History No. 860423; University of Texas at El Paso No. 11108; Florida Museum of Natural History No. 122793; Universidad Nacional Autonoma de Mexico No. 1210; Field Museum of Natural History No. 208712; Walter B. Miller No. 7341.

Etymology: This species is named for my long-time friend and mentor, Dr. Walter B. Miller. I have benefited greatly from his insights and direction.

Discussion: There are, at present, six known extant species of *Holospira* occurring in Sonora (BEQUAERT & MILLER, 1973:142–143). These species, which include the primarily Arizonan *H. ferrissi* Pilsbry, 1905, are members of three subgenera.

Because it has a quadrilamellate shell, *Holospira* ***milleri*** is assigned to the subgenus *Holospira s.s.* The only other Sonoran (and Sinaloan) species in this subgenus is *H. cyclostoma* Pilsbry, 1953. The shell of *H.* ***milleri*** is similar to *H. cyclostoma* in size, and in the number of whorls. However, it differs by being thinner and more gradually tapered, and by possessing extremely convex whorls. In addition, *H. cyclostoma* was collected in drift material from arroyos near San Bernardo in southern Sonora and along the Rio Fuerte near San Blas in northern Sinaloa. These drainage systems are separate from the Rio Yaqui and ca. 200–275 km south of El Novillo. Since it is well known that most *Holospira* species are extremely localized in distribution, it is considered highly improbable that they could interbreed.

The remainder of the Sonoran species (excluding *Holospira ferrissi*) have one internal lamella (the axial), or none, as in *H. minima,* and are assigned to the subgenus *Allocoryphe.* The shell of a subspecies of one of these, *H. dentaxis striatella* Pilsbry, 1953, is similar in external appearance to *H.* ***milleri.*** It, too, is somewhat translucent and has strongly convex whorls; however, it is more strongly and vertically costate.

Holospira ***milleri*** is unique among *Holospira* species known thus far in regard to the reproductive anatomy by possessing a verge in the penial complex. It should prove interesting to see if *H. cyclostoma* has a verge.

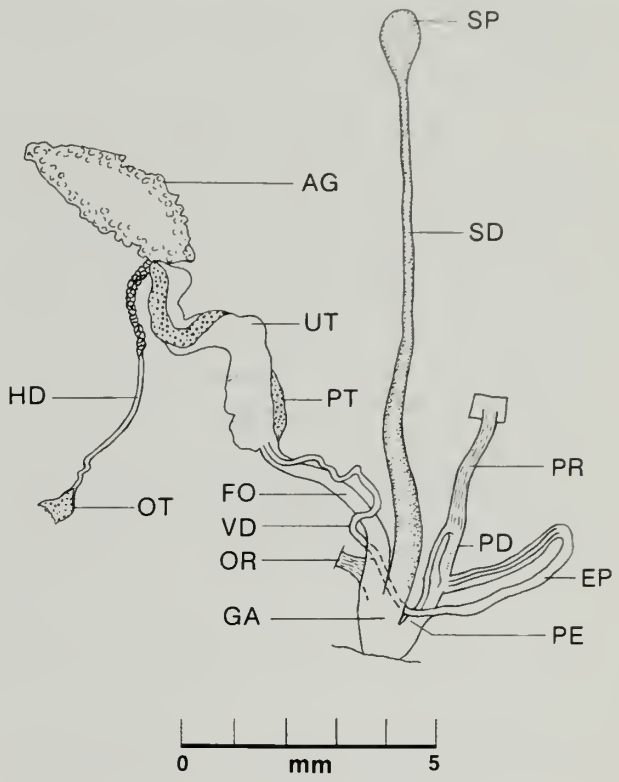

Figure 3

Reproductive system of *Holospira minima.* Specimen collected at Cerro de la Campana, Hermosillo (the type locality), by L. H. Gilbertson, 16 May 1987. Shell broken for dissection. AG, albumen gland; EP, epiphallus; FO, free oviduct; GA, genital atrium; HD, hermaphroditic duct; OR, oviducal retractor muscle; OT, region of ovotestis; PD, penial diverticulum; PE, penis; PR, penial retractor muscle; PT, prostate gland; SD, spermathecal duct; SP, spermatheca; UT, uterus; VD, vas deferens.

With 45 teeth per row, the radula of *Holospira* ***milleri*** is distinctively different from the radulae of the two other species in the subgenus *Holospira s.s.* for which the radula has been described, specifically *H. goldfussi* (Menke, 1847), and *H. nelsoni* Pilsbry, 1903, which have 53 and 55 teeth respectively (PILSBRY, 1903:69). Rather, it falls within the range of teeth found in species of the southern Mexican subgenus *Bostricocentrum* Strebel, 1880, which have 39–45 teeth per row (THOMPSON, 1964).

As expected, based on significant differences in shell morphology, the reproductive anatomy of *Holospira minima* (Figure 3) differs in several obvious respects from *H.* ***milleri.*** The male genitalia are larger, and its tubular epiphallus joins the penis laterally, thereby forming the penial diverticulum. The penial retractor muscle is wider, and inserts upon the apex of the penial diverticulum rather than upon the epiphallus as in *H.* ***milleri.*** Also, *H. minima* lacks a verge. Because of these anatomical differences, along with those of the shell, these two species apparently

have had distinctly divergent phylogenies. Their anatomies are similar in one important respect, however, that of lacking a spermathecal diverticulum.

ACKNOWLEDGMENTS

I wish to express my sincere thanks to Diana Warr, Edna Naranjo-Garcia, and especially James E. Hoffman for their assistance and camaraderie at the University of Arizona, to Mary A. Garback, and Mary K. Dill at the Academy of Natural Sciences of Philadelphia for the loan of numerous holotype and paratype shells of Sonoran *Holospira* species, to Dwayne Moses for the drawings of the reproductive systems, to my wife, Nancy, and son, Scott, for accompanying me to Sonora, and to the Board of Trustees of the Coast Community College District for the privilege of a sabbatical leave during which time this research was undertaken. I am especially grateful to Dr. Walter B. Miller for sponsoring me at the University of Arizona, and generously providing me with his personal books and collections. He prepared the stained, slide-mounted reproductive anatomy of *H. **milleri*** that is figured and described herein. He (along with E.N.-G. & J.E.H.) accompanied me to the site of *H. **milleri***, and identified the plant species.

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Morphology and Anatomy of a New Iberian Species: *Deroceras geresiensis* (Gastropoda: Pulmonata: Agriolimacidae)

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Abstract. Periodic, systematic sampling of the western Iberian Peninsula, comparison of specimens collected with topotypes of *Deroceras lombricoides* (Morelet, 1845), and analysis of the descriptions of *D. lombricoides* given by Morelet and Simroth have shown that Simroth's description of this species is confused with that of a quite distinct agriolimacid characterized by two glandular spheres on the distal penis, each of which houses a tongue-like stimulator. The morphology and anatomy of this second species, which we consider as new to science, are described and compared with those of other species living in the same region. We also report what appears to be its present distribution.

INTRODUCTION

In describing the copulation of *Deroceras lombricoides* (Morelet, 1845), SIMROTH (1891) stated that the pair took up positions next to each other forming a circle, and that they each produced, from the genital orifice, a stimulator consisting of a thick flat triangular lip with which they touched each other's back (SIMROTH, 1891:pl. 3, fig. XI). A few lines later, however, he described different mating behavior in a pair observed in Oporto: these slugs alternately moved round in a circle and stayed still, the stimulator remaining in contact with the mate all the time. Drawings of this latter copulation were provided (SIMROTH, 1891:pl. 3, figs. XIII–XV), but not of the mating slug's genitalia, though in the text it is mentioned that when the specimens were placed in alcohol, one of them evaginated a kind of "spoon," round outside and concave inside, whose tip exhibited pale epithelial formations differing from the rest of the evaginated structure. Simroth regarded this structure as a stimulator related to two whitish vesicles observed during copulation.

Examination of topotypes of *Deroceras lombricoides* has led us to the conclusion that Simroth's description and drawings of the copulation of this species (SIMROTH, 1891: pl. 3, figs. XI–XVI) refer to two quite distinct species: figs. XI, XV, XVIa, and XVIb depict *D. lombricoides s.s.*, but figs. XII–XIV show a different species that, as Simroth himself noted (SIMROTH, 1891:285–286), was characterized by two glandular spheres on the penis, each containing a stimulator. Sampling of several sites in Portugal has yielded 97 specimens of this latter species. After examination of its anatomy and copulation (which was photographed), we conclude that it is a new species, and we here name it.

Deroceras ***geresiensis***
Rodriguez, Castillejo & Outeiro, sp. nov.

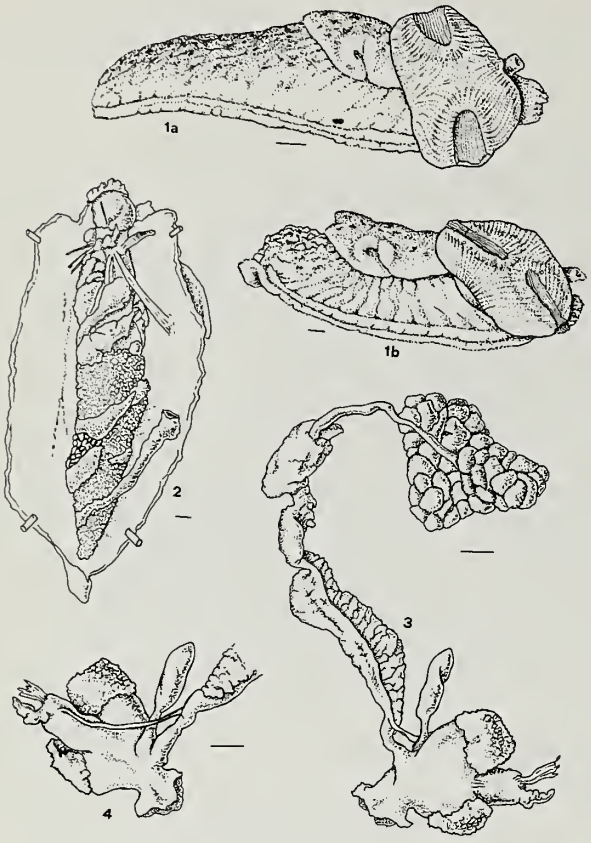
(Figures 1–42)

Diagnosis: External anatomy, limacella, pallial complex, and internal topography all common to other species of the same genus. Differences: penis divided in a voluminous anterior region with two spheres of glandular appearance, and a cylindrical posterior region with a short, wide caecum on which the vas deferens end; two stimulators, tongue-shaped, located in the roof of the penial sphere; penial gland (=flagelliform appendices) terminal, subdivided into two or three festooned diverticula of variable length.

Description: Length *in vivo* up to 30 mm, length in 70% alcohol up to 22 mm (Figures 1a, b). Back dark chestnut in color, lighter at sides and neck. Epidermis irregularly speckled with darker spots. Sole whitish, divided into three regions. Body mucus colorless.

Organs *in situ*: Organs exhibiting topography characteristic of the genus (Figure 2). Intestine with three circumvolutions, rectum with no caecum. Ovotestis to the left of the last one-third of the visceral sac, approaching the rectum ventrally. Conjunctive tissue enveloping the visceral sac colorless.

Pallial complex (Figure 5): As in other species of the genus. In the paratype depicted here, kidney lobe projecting over the rectum smaller than in other specimens.



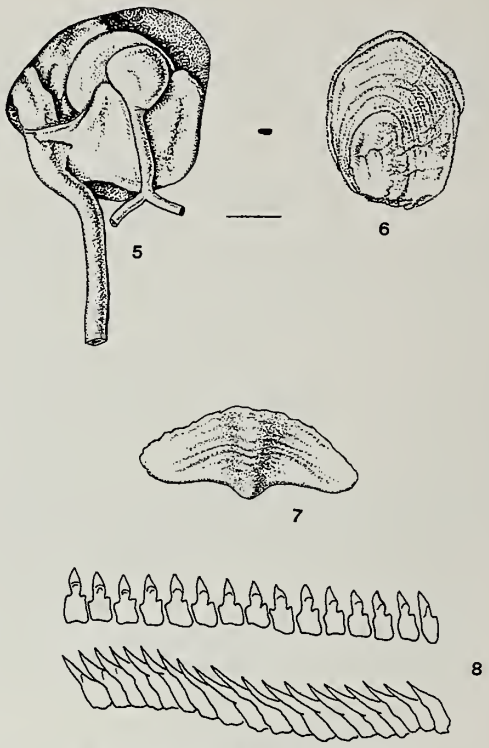
Explanation of Figures 1 to 4

Deroceras ***geresiensis*** Rodriguez, Castillejo & Outeiro, sp. nov.

Figures 1, 2. Specimens with the distal penis evaginated. 1a. Paratype from Taipas in the hills around Braga. 1b. Paratype from Pontefeia, Serra do Gerês. 2. Holotype, organs *in situ*.

Figures 3, 4. Holotype, dorsal and ventral views of the genitalia.

Scale, 1 mm.



Explanation of Figures 5 to 8

Deroceras ***geresiensis***. Paratype from Pontefeia.

Figure 5. Pallial complex.

Figure 6. Limacella.

Figure 7. Mandible.

Figure 8. A row of teeth.

Scale, 1 mm.

Limacella (Figure 6): Roundish, very fragile, with a subterminal nucleus.

Mandible (Figure 7): Oxygnate.

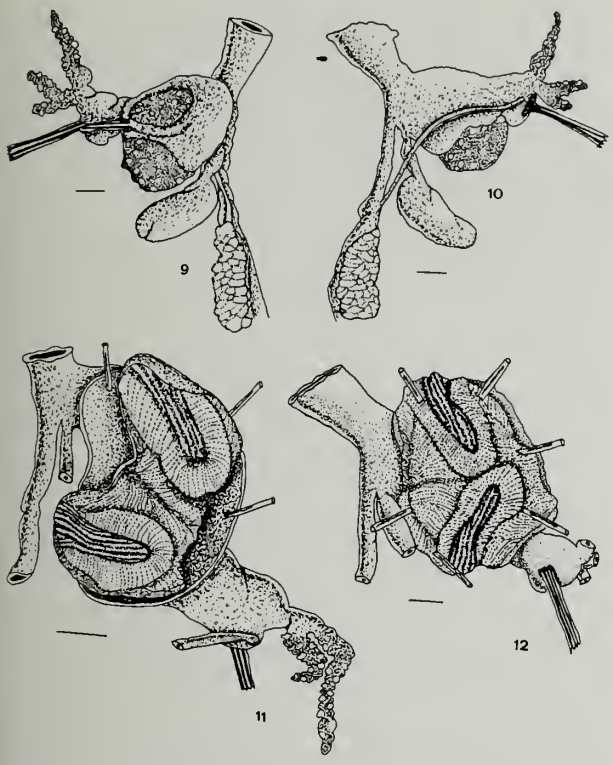
Radula (Figure 8): Central teeth tricuspid, lateral ones bicuspid, and marginal ones monocuspid. Formula: (C/3 + 12–13/2 + 21/1) × 94.

Genitalia (Figures 3, 4, 9–12): Ovotestis formed by black acini in sexually mature individuals. Topography of the hermaphrodite duct, albumin gland, and spermoviduct characteristic of the genus.

Proximal penis cylindrical, with a slight subterminal swelling. Penial gland terminal, divided in two or three branches of variable length with festooned margins. Distal penis thick, spheroid, with two globose masses of glandular appearance. Vas deferens short, not variable in caliber, ending on the penial body below the penial gland near the insertion of the penial retractor muscle. The latter long, inserted at one end near the pallial complex; at the other end it bifurcates, one branch being inserted on the proximal portion of the penis and the other near the base of the spheroid masses.

Bursa copulatrix ovoid, with a short duct. Free oviduct, as long or longer than the bursa copulatrix duct. Internal wall of the penis lined with fine longitudinal grooves continuing into the walls of the spheroid masses. The roof of each of these masses exhibiting a tongue-shaped, more coarsely grooved stimulator at the tip of which the external glandular mass. Only the distal penis protracted during copulation, on which occasion the stimulators and the orifices communicating the glandular masses with the inside of the penis clearly visible. The stimulators well differentiated in sexually mature individuals only; immatures exhibit triangular areas in which the epithelial grooving differs of the rest of the penis.

Etymology: This species has been named *Deroceras geresiensis* because it was collected in the Serra do Gerês, Portugal.



Explanation of Figures 9 to 12

Deroceras ***geresiensis***. Genitalia of paratypes from Pontefeia.

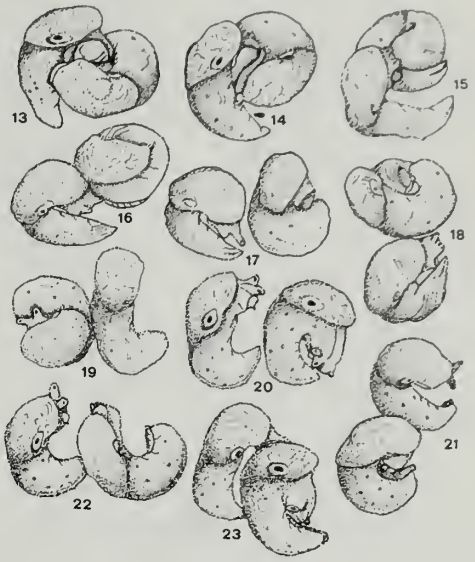
Figures 9, 10. Dorsal and ventral views.

Figures 11, 12. Interior of the distal penis showing the two stimulators.

Scale, 1 mm.

Material examined (Figure 43): *Holotype:* Curral de Leonte, Serra do Gerês (Portugal, U.T.M. 29TNG72), *leg.* J. Castillejo, 1 Nov. 84. Deposited in the Natural History Museum, Madrid, Spain (NHMM).

Paratypes: 18 specimens collected in the same site and in the same day as the holotype: 4 of NHMM, 5 in the Luis Iglesias Museum, Santiago (LIMS), 2 in the collection of the Zoology Department, University of Santiago de Compostela (ZDUS); 7 in the Natural History Museum, Wroclaw, Poland (NHMW). Pontefeia, Serra do Gerês (Portugal, U.T.M. 29TNG72), 9 Feb. 84, *leg.* J. Castillejo (4 specimens ZDUS, 2 spec. in the collection of Dr. Giusti, Siena, Italy (CGMI). 1 Nov. 84, *leg.* T. Rodríguez (4 spec. ZDUS). Feitos, Barcelos (Portugal, U.T.M. 29TNG20), 31 Oct. 84, *leg.* A. Outeiro (4 spec. ZDUS). Taipas, Mountain of Braga (Portugal, U.T.M. 29TNF59), 14 Dec. 85, *leg.* J. Castillejo (6 spec. ZDUS, 1 spec. CGMI). Pintos, Pontevedra (Spain, U.T.M. 29TNG39), 1 Mar. 84, *leg.* J. Castillejo (38 spec. ZDUS, 4 spec. CGMI); 28 Sept. 86, *leg.* T. Rodríguez (7 spec. ZDUS). Arbo, Pontevedra (Spain, U.T.M. 29TNG56), 1 Mar. 84, *leg.* J. Castillejo (6 spec. ZDUS).



Explanation of Figures 13 to 23

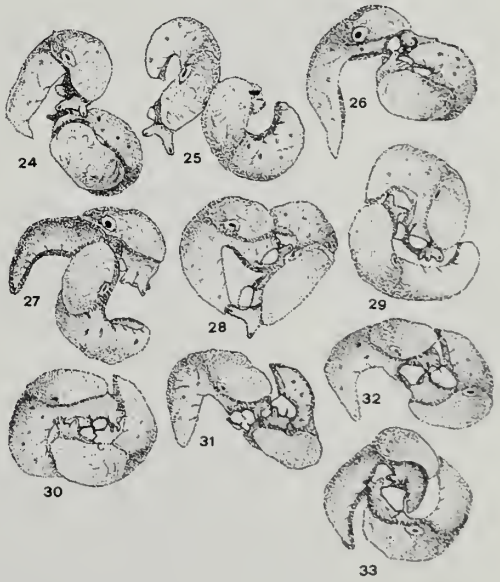
Deroceras ***geresiensis***. Copulation of two paratypes from Curral de Leonte.

Figures 13, 14. First phase.

Figures 15–18. Second phase.

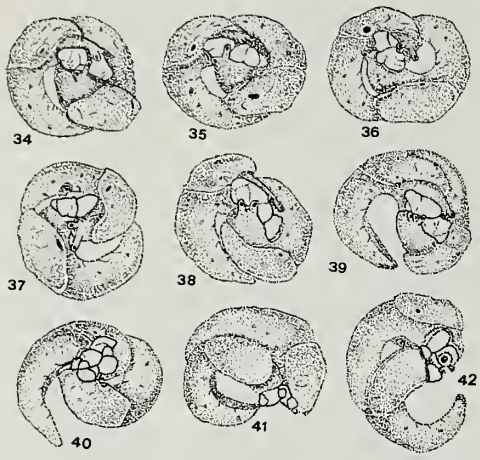
Figures 19–23. Mixed phase.

Copulation: The copulation described here was observed on 1 November 1984 in the Serra do Gerês (Portugal), in the locality named Curral de Leonte. The drawings are based on photographs taken *in situ*.



Explanation of Figures 24 to 33

Deroceras ***geresiensis***. Copulation continued from Figures 13–23, with progressive evagination of the stimulators.



Explanation of Figures 34 to 42

Deroceras ***geresiensis***. Copulation continued from Figures 24–33.

Figures 34–36. Build-up towards maximum evagination of the penis.

Figures 37–39. Initiation of sperm exchange.

Figure 40. Sperm exchange.

Figure 41. Initiation of invagination of the penis.

Figure 42. End of copulation; the stimulators are invaginated and the two animals part.

The two specimens were found head to tail forming a "C," their flanks in close proximity, under a stone near a natural meadow. The duration of the copulation is not known with accuracy, since its preliminary stages had already been completed when the pair were surprised. A few minutes after their discovery (Figures 13, 14), the two specimens parted (Figures 15–17), their genital atrium remaining evaginated. On separating, they remained side by side while each chased its own tail clockwise and licked its tip (Figure 18). After placing their flanks in contact (Figure 19), they resumed their tail-chasing, their sides touching from time to time (Figures 20–23). They then touched head to head (Figure 24) before continuing to chase their own tails side by side. This behavior was followed by contact between the partially evaginated genitalia (Figures 26, 27); after licking each other in the neighborhood of the genital orifice (Figure 28), they again placed their genital atrium in contact (Figures 29, 30); the evagination of the genitalia followed, so that two concave, linguiform structures (stimulators) appeared (Figure 31). This initiated a phase of much closer contact during which they continued to move clockwise in a circle while the distal portion of the penis was slowly evaginated (Figures 32–39). The distal penis became turgid, and two yellowish masses with the stimulators at their bases appeared on each animal (Figure 40). At this point the stimulators and yellow masses of each animal locked with those of the

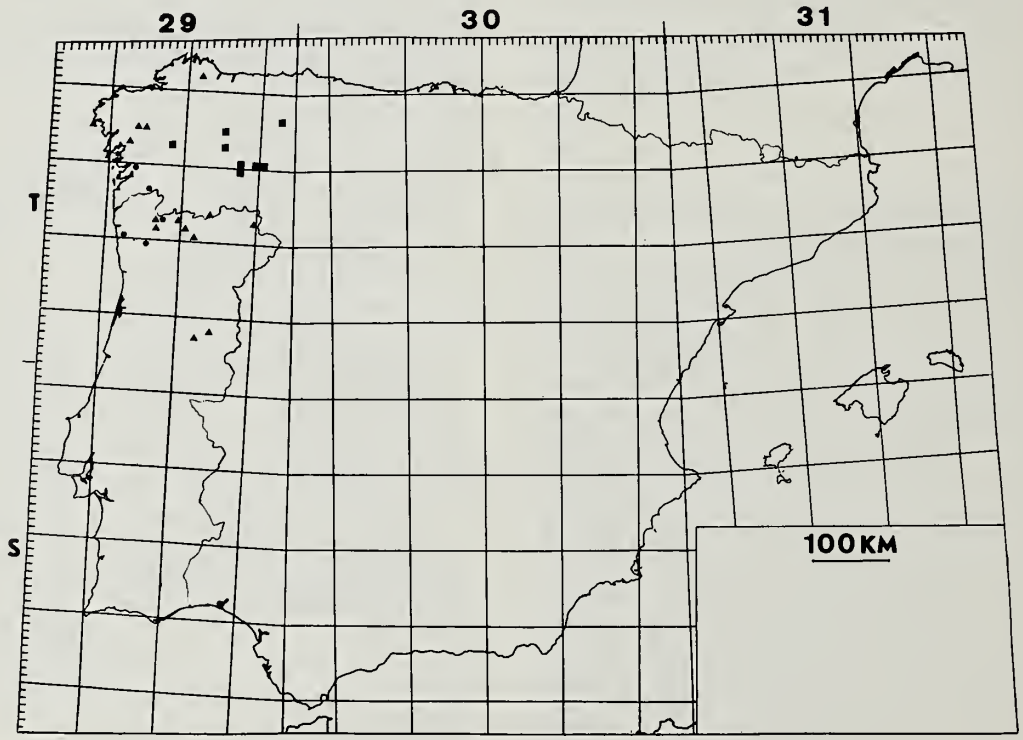


Figure 43

Map of the Iberian Peninsula, showing localities where *Deroceras* ***geresiensis*** (●), *D. lombricoides* (▲), and *Furcopenis darioi* (■) have been found.

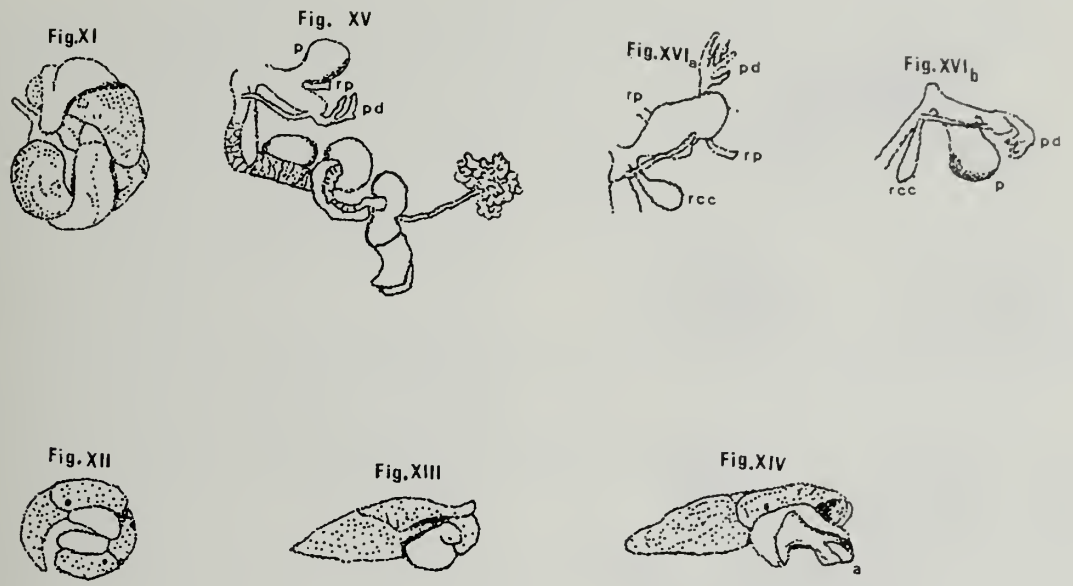


Figure 44

Part of plate 3 from SIMROTH (1891) with drawings of the genitalia and copulation of *Deroceras lombricoides* (Morelet, 1845).

other, and whitish trickles of sperm were rapidly exchanged. After this phase each specimen entirely covered itself with colorless, runny mucus. Once copulation was completed, the mucus-covered individuals gradually separated (Figures 41, 42), slowly invaginated their penes, and moved off in different directions.

In the above copulation, three phases can be distinguished. In the first, the two individuals indulge in mutual contact during which they place their genitalia, heads, or sides in contact, or lick the other's genital orifice area. In the second phase each chases and licks its own tail, though contacts with the mate also take place. During the observed copulation, these two phases were repeated in turn a total of three times. During the culminating third phase, exchange of sperm took place as described above.

→

Figure 45

Furcopenis darioi Castillejo & Wiktor, 1983. A–E. External morphology and genitalia of topotypes from Seoane, Sierra del Caurel, Spain (21 Dec. 84, *leg.* A. Outeiro). F. Spermatic mass found in the bursa copulatrix of the specimen depicted in Figure 46H. Scale, 1 mm.

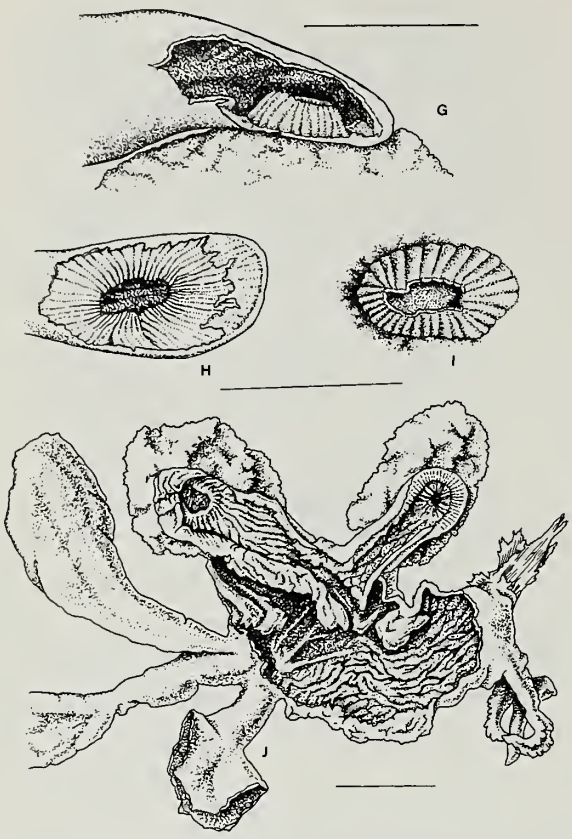


Figure 46

Furcopenis darioi Castillejo & Wiktor, 1983. Topotype from Seoane, Sierra del Caurel, Spain (21 Dec. 84, *leg.* A. Outeiro). G–I. Communication between the accessory organs and the accessory gland. J. Inside of the penis and accessory organs. Scale, 1 mm.

DISCUSSION

According to F. Giusti (personal communication, 1985), *Deroceras* ***geresiensis*** is possibly identical to *D. lombricoides* (Morelet, 1845).

Deroceras lombricoides, which has recently been re-described by CASTILLEJO *et al.* (in press), is characterized by a distal portion of the penis showing a spheroid swelling covered with a horseshoe-shaped mass of glandular tissue and housing a horseshoe-shaped stimulator corresponding to SIMROTH's (1891) description of a "pleated comb twisted upon itself many times." CASTILLEJO *et al.* (in press) also observed populations in which the free end of the stimulator was less marked, so that the stimulator became the flat fold that is characteristic of *D. immaculatum* Simroth, 1891. The difference between *D. lombricoides* and *D. geresiensis* lies in the penis: in the last species the spheroid anterior portion shows two glandular masses, each communicating with a internal tongue-like stimulator.

The pair found copulating in the Serra do Gerês (1 Nov. 84) was originally classified by CASTILLEJO & MASCATO (1987) as *Furcopenis darioi* (Figures 45, 46), a species characterized by two accessory organs on the distal portion of the penis, each tipped with an accessory gland communicating with the inside of the organ via a hollow cone with the accessory gland at its base (Figures 46g–i). *Deroceras* ***geresiensis*** has no accessory organs, and the glandular masses on its penis communicate with the inside of the penis via a lanceolate area exhibiting coarser grooving than the rest of the penis. Examination of new topotypes of *F. darioi,* and re-examination of the paratypes deposited in the Zoology Department of the University of Santiago de Compostela (Spain), have confirmed that the accessory bodies are a constant feature even among juveniles, so that it hardly seems possible that their absence from the specimens described here as *D.* ***geresiensis*** can be due to intraspecific variation. The geographical distribution of the two species is likewise different: *F. darioi* has so far been collected only in soils developed from schists in El Bierzo (León, Spain) and neighboring areas, whereas *D.* ***geresiensis*** is a more coastal species found only in granitic soils of the Portuguese Costa Verde and the south of the Spanish province of Pontevedra. No specimens of either species have been found at sampled sites between these two territories.

Finally, *Deroceras* ***geresiensis*** is differentiated from *D. dalmatinum* Grossu, 1972, by having its two stimulators located symmetrically on the proximal penis, whereas *D. dalmatinum* has a papillose stimulator on the proximal penis and a curved stimulator on the distal penis.

ACKNOWLEDGMENT

We thank Dr. Giusti and Dr. Wiktor for advice on the taxonomic revision of material utilized for this paper. We thank Dr. Giusti for the critical revision of this manuscript.

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The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

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References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.*, 1953).

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a) Periodicals

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b) Books

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c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

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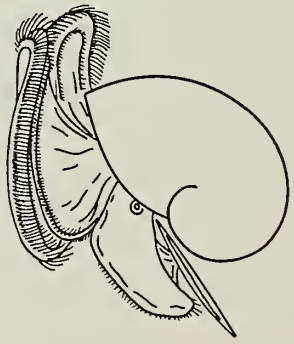

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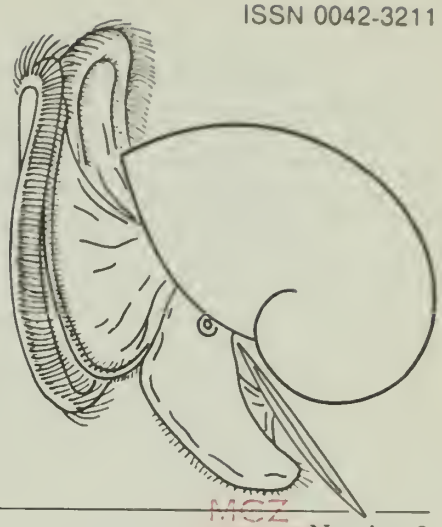

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The Veliger is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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A Personal History of *The Veliger* and The California Malacozoological Society, Inc.

by

JEAN M. CATE

P.O. Drawer 3049, Rancho Santa Fé, California 92067, U.S.A.

As one of the few persons still available who remember the beginnings and subsequent growth of *The Veliger,* I have been asked to set down my recollections of its first 25 years. I am proud to have been involved over the years in several different ways with *The Veliger* and its governing body, the California Malacozoological Society, Inc. (CMS) (Table 1).[1] Since its modest beginning in 1958, the developmental stages of *The Veliger* may be likened in some ways to those of a molluscan veliger, and it has been my privilege to watch this small hatchling become a thriving adult—a credit to its founder and to those who worked in its behalf.

The title, "The Veliger," was chosen by its founding Editor, Dr. Rudolf (Ruedi) Stohler (Figure 1), University of California at Berkeley (UCB), because from its outset he "hoped it would always continue to grow." Pronunciation of the word "veliger" is variable, even among biologists, as VEH' lih jer; VEL' ih gur; VEE' lih jer; and VEE' lih gur.

The Veliger's logotype represents the veliger of an unknown species of the gastropod genus *Crepidula,* drawn by Mrs. Emily Reid (Figure 2) (UCB). Based on her drawing, the masthead was designed by Amadeo Tomassini, a typographic artist in the Printing Department of UCB who designed the United Nations Charter in 1948.

In 1952, a group of shell collectors in the Berkeley area formed the Northern California Malacozoological Club (NCMC). Monthly meetings were held at the Oakland Museum; annual dues were $1.00. Dr. Rudolf Stohler was the club's scientific advisor and a charter member. In 1956, as the group grew and space at the museum became inadequate, its meetings were moved to the Life Sciences Building (LSB) on the UCB campus.

The first mimeographed issue (Volume 1(1)) of *The Veliger* was published as the newsletter of the NCMC on 27 June 1958. Helen Hunt was Editor; stencils were typed by Dr. Stohler's daughter Heidi on an ordinary typewriter, typing them twice in order to achieve two nearly justified columns on each page. Volume 1(1-4) contains a total of 40 pages.

Metamorphosis of *The Veliger* began when Volume 2(1) (July 1959) was published. Although the body of the text was still mimeographed, end papers and a new granite-paper cover were now printed by Dr. Stohler with hand-set type on a hand-operated press at his home. For the first time, a black and white halftone plate was included, in a paper on California oysters by Dr. Leo G. Hertlein of the California Academy of Sciences (CAS) (HERTLEIN, 1959). The quality of the halftones improved with each new issue. Heidi still typed the text, and Ruedi was the new Editor. By publishing professional-quality papers from Dr. Myra Keen of Stanford University (SU), Dr. Hertlein, and others, Ruedi had started fulfilling a lifelong dream of producing his own journal.

Distribution of that particular issue is still a vivid memory. At approximately 12:05 a.m. on 30 June 1959, the journal was slipped under the bedroom doors of all those attending the annual conference of the American Malacological Union, Pacific Division, at Asilomar, California. Many of us were still awake, visiting friends and making considerable noise. When we heard the "whoosh" of paper sliding under our door, we went to see who could be there at that hour, expecting to be asked to quiet down.

The opened door revealed a smiling Ruedi Stohler, the delivery person of Volume 2(1). It bore the date July 1, 1959; by way of the early morning delivery, he had maintained the taxonomic integrity of the legal publication date. Free to non-subscribers, that issue introduced *The Veliger* to a large new audience.

During that volume-year (fiscal 1959-1960), other ma-

[1] Abbreviations used: 1(1)—Volume 1, No. 1 (etc.); BML—Bodega Marine Laboratory; CAS—California Academy of Sciences; CMS—California Malacozoological Society; LACM—Los Angeles County Museum of Natural History; LSB—Life Sciences Building, University of California, Berkeley; NCMC—Northern California Malacozoological Society; SU—Stanford University; UCB—University of California, Berkeley; UO—University of Oregon; WSM—Western Society of Malacologists.

Figure 1

Dr. Rudolf (Ruedi) Stohler, founding Editor of *The Veliger*; photograph by James H. McLean.

jor changes took place. The Northern California Malacozoological Club was incorporated under California law as a non-profit educational corporation, to protect its members from individual lawsuits. (Although an unincorporated club's members can be sued separately and collectively if someone is injured during a club-sponsored event such as a field trip, a corporation can be sued for no more than the amount of its assets.)

I have special reasons to remember the Volume 2(4), April 1960 issue. In it my husband Crawford and I, with our friend Cliff Weaver of Hawaii as co-author, proudly published our first scientific paper. It concerned the identification of *Cypraea ostergaardi* Dall, 1921, placing *C. alleni* Ostergaard, 1950, in synonymy (CATE, C. N., *et al.*, 1960). By then I was well enough acquainted with Ruedi Stohler to mention that Cliff Weaver's name had been misspelled on the cover, and that there were two typographical errors in the text. Suddenly I was Assistant Editor, with the job of proofreading each issue. At Volume 6, I was officially elevated to Associate Editor. My name now appeared on the cover, and my "salary" was increased by adding another zero each year. We joked a good deal about that nonexistent salary; I was worth every zero of it. (The proofreading job continued for 27 years, from Volume 3(1) through Volume 29(4). By then the new Editor, the authors, and the readers at Allen Press [our present printers] had been checking the proofs for 4 years; having become redundant, I retired from that appointment.)

NCMC's annual dues, now called subscriptions, were raised to $2.50 for Volume 3. An Editorial Board was appointed; its roster of ten distinguished scientists appears inside that volume's front cover. These are the referees to whom papers submitted to Dr. Stohler for publication were referred for review, prior to acceptance or refusal.

Volume 3(1) (July 1960) found the Editor's office at LSB resplendent with a new IBM® electric typewriter, the latest word in technology. Both Ruedi and Heidi used it to prepare the now-longer issues; it was a giant step forward, automatically producing fully justified margins and giving the journal a more professional appearance. The issues were no longer mimeographed, but offset by the UCB Printing Department, and the finished pages were then delivered to Ruedi's home.

Depending upon the size of the issue and number of reprints ordered, somewhere between 20 and 30 cartons of pages were delivered; that is approximately 200 to 300 reams of paper, all extremely heavy. Some, containing halftone plates on coated stock, were even heavier. Total weight of all the finished pages was somewhere between 490 to 735 kg per average issue; the mailbags, containing nearly 1000 processed issues plus authors' reprints, weighed a good deal more.

Circling his dining room table, Ruedi collated each issue and the authors' reprints by hand. Collating one average issue of 100 pages or so and its concomitant reprints required a 10-km circuit. He also performed all the mailing tasks, filling mailbags with issues he had stuffed into preaddressed envelopes and sorted by zip code. The stacks of mailbags filled the Stohlers' front hallway before delivery to the post office on publication date, having been moved from house to car in countless trips with a little red wagon. Ruedi also typed, addressed, and mailed invoices printed on his small press. This routine continued through 25 years, growing larger year by year as the journal grew.

In those early years, I flew from Los Angeles to Berkeley on a quarterly basis as each issue's preparation drew to a close. Every morning, Ruedi settled me into some available vacant room in LSB, where I corrected the proofs without access to a dictionary or other references. He brought new batches daily, picking up the previous day's edited pages and bringing new ones to read, along with corrections to be checked again. Each issue's stint required three or four days' work; time permitting, it was usually read through twice. At press-time, we offered a hopeful toast (in diet soda) for a perfect issue, free of typographical errors.

The most important event of all came with Ruedi's purchase in Los Angeles of a decrepit, 30- to 40-year-old, but operative, Mergenthaler® Linotype© machine prior to the start of Volume 6(1) (1963). It was a great bargain, its market value then being about $10,000 to $15,000, whereas its cost was only $1800. During the first few years he used it, Ruedi personally added four times that amount to its value by purchasing new matrices, extra Linotype® magazines, kerned ligatures, dingbats, and specialized fonts; everything possible was done to improve the product typographically.

Figure 2

Mrs. Emily Reid (left); photograph by Phyllis Thompson-Spowart. Mrs. Jean M. Cate (right); photograph by Jennifer Nelson.

Since it was not feasible at that time to move the Linotype® machine to Berkeley, Crawford and I searched for low-rental properties reasonably near our home, such as vacant garages and store-front buildings. Not finding a suitable location, we finally added a building on our property to house the huge machine. It also held a screeching metal-cutting printer's saw to cut lead slugs of cold type for tabular material; wooden storage cabinets to hold printer's chases, both full and empty; and a small work area for page make-up, the carpentry having been done by Ruedi and hauled to Los Angeles in his car.

With the building completed, the Linotype® machine was installed and Ruedi went home to put the next issue together in the old typewritten way, as it was too close to the next deadline to risk a breakdown on the unfamiliar machine.

During Ruedi's absence, Crawford and I carefully covered the Linotype® machine, later dubbed "The Beast," with a plastic dropcloth to ward off dust. We didn't realize that the extra-thick concrete floor, designed to hold the 3000-kg machine, had not completely cured as a floor of normal depth would have done by that time. We had thus created an efficient, constant vapor-bath under the dust cover while the concrete slowly dried beneath it for several weeks. This caused rust in all the many nooks and crannies of the contraption, but there wasn't a speck of dust on it.

We were stunned when we saw what had happened. Ruedi didn't scold, but went directly to work dismantling the machine and removing the rust—a monumental job. After thorough cleaning, it was overhauled by a specialist. Ruedi's next step was to learn to repair it, and repair it he did, over and over again, throughout its existence. Starting with Volume 6 and its supplement, 20 volumes and 8 supplements were produced on The Beast, though not without innumerable breakdowns during its many years of service.

Ruedi was at work shortly after 4 a.m. each day, having risen at 3 to light the fire under the lead-melting pot. Later an automatic timer-thermostat was installed to light the gas flame at 3 a.m., thus giving him an extra hour of sleep while the lead melted. When the supply of lead ingots was depleted, he melted down batches of used type-slugs, with approximately one large meltdown per issue. By adding a toner containing zinc and antimony to the molten lead, he created new ingots in iron molds, thereby recycling the old ingots several times. There was, of course, constant exposure to the lead fumes whenever the machine was operating—a serious health hazard. A fan and air conditioner were installed to help expel the fumes, but they did not totally alleviate the problem.

Typesetting for each issue required about 3 weeks of very long days. When the pages were nearly ready, Ruedi placed the heavy load of printer's chases full of type in his 27-year-old Chevrolet for the 312-km drive north.

To complete the issue, each page was carefully composed, not only according to its content, but also to balance attractively. Blocks of wood in various sizes and shapes were inserted in the made-up page of type, leaving uninked

spaces on the "repro" proofs to allow for adding tabular matter and text figures. The text was spaced out, by hand, with slim strips of paper and board so that both columns would come out even at the bottom of each page. The pages of type were then inked, pulled, proofread, and corrected. Then, at last, the final repro proofs were run. These went next to Emily Reid for final pasteups. At this stage, the UCB Printing Department took over for the offset process, and when the finished product was delivered to Ruedi's home, the collating began, again.

Emily Reid holds a very special place in the history of *The Veliger,* though she has always worked quietly in the background, with little public knowledge of the important rôle she played in our production. After producing the logo, she soon became irreplaceable in other areas as well. From the first illustrated issue, Volume 2(1), she did all the graphics: pasting up photos, labeling tables, illustrative plates and charts—always matching in both style and scale with the journal, Ruedi having supplied appropriate printed letters and words in the journal's Baskerville© type style. She also provided meticulous drawings, and excellent maps for type localities and other uses; many authors engaged her work to illustrate their papers. Emily was unquestionably an essential part of the staff, volunteering her time and impeccable talent to help achieve and maintain our high standards for over 25 years. From the start, she was indispensable in making *The Veliger* a journal of the highest quality.

The year 1961 brought an innovation to the pages of *The Veliger*: color plates. Dr. G Dallas Hanna of CAS was then developing a new process of printing color plates, using an extremely fine, 300-line screen—the first time color separations of that high quality had been produced. He kindly furnished us with sample runs at cost; we paid only for the paper, ink, and other production costs—a great bargain, at $100 per plate. The exact superimposition of colors known as "register" is so critical at the 300-line level that Mrs. Margaret Hanna, working alongside her husband, carefully scrutinized the register of each plate and destroyed all that failed to measure up to their exacting standards. The first of these plates appeared in *The Veliger* as Plate 1 in Volume 4(1). Such fine screens are no longer in use today in the United States for commercial color work, as their production is so difficult that the cost is prohibitive. Sharing that privilege with CAS, *The Veliger* had the benefit of Dr. Hanna's labor and his unique system for a few years, and published several color plates.

One of the most important developments in *The Veliger*'s metamorphosis occurred during Volume 6(3), when what might be called its vestigial operculum was shed. In 1963, members of the Northern California Malacozoological Club (NCMC) made it known that they could no longer manage the burgeoning business of *The Veliger*. Business management of the journal had become too big a burden for the NCMC to carry any longer. The club left its newsletter in Dr. Stohler's care, to revert to being a shell club, not publishers of a scholarly journal. An amicable agreement was made, with *The Veliger* assuming all assets and liabilities of NCMC pertaining to *The Veliger,* and relinquishing claim to its accumulated library materials. Assets included the Veliger Endowment Fund and the Veliger Operating Fund, plus all back issues of the journal—a total value of less than $3000. The printing machinery and equipment were Dr. Stohler's personal property.

A new organization was now needed to manage development, business affairs, and the fiscal assets of *The Veliger*. Preliminary plans were made, and the framework of the new society was ready by the time legal details of its incorporation were completed. On 21 December 1963, The California Malacozoological Society (CMS) was organized, a similar name purposely being chosen to reflect credit on NCMC. Twelve charter members were named, and officers elected (Table 1). Incorporation was discussed, and committees were formed for Bylaws, Finance, and Publication. The cost of incorporation was shared by the charter members, requiring a donation of only $5.00 each, thanks to the kind assistance of Attorney Harry Poppic, who had also donated his services earlier for NCMC.

Two classes of membership were named: Regular Members, with voting rights on the Executive Board, and Affiliate Members, without vote. Affiliate Members are individuals who receive the journal with paid-up membership in the Society. A third category, Subscribers, includes non-member institutions such as libraries, museums, and universities.

The two funds acquired from NCMC, the Endowment Fund and the Operating Fund (the early earnings of the journal), were established as the financial basis of the new corporation. The Endowment Fund's assets are derived from donations and other sources; only the income from its principal is available, and it is designated solely for the expenses of publishing the journal. The Operating Fund—fed by income from the Endowment Fund and such other sources as membership dues, subscriptions, designated contributions, sales of reprints, supplements and back issues—pays all expenses connected with publication and distribution of *The Veliger*.

Incorporation and bylaws were both completed by 4 February 1964. Annual dues were set at $5.00 for Volume 7. In March, the society was granted both federal and state tax-exempt status as a non-profit, scientific educational corporation; "Inc." became a part of our official title and the new corporate name appeared for the first time in November 1964, on the cover to the Supplement to Volume 6. The first three Trustees (Table 1), on a revolving 3-year schedule, were elected from among the Regular Members during March. The duty of the Trustees is to administer the Endowment Fund, the principal of which is unavailable without their signatures.

Until now, our state charter's tax-exempt clause, an inherent part of the state law on non-profit businesses, had not held a special meaning for *The Veliger,* not being a factor in a shell club's ordinary business. Lacking a product to sell, a shell club pays no sales tax, and seldom

Table 1

Executive Board members, California Malacozoological Society, Inc.

Charter Members, 21 December 1953

President: Dr. Cadet Hand,* UCB; Bodega Marine Lab.
Vice President: Allyn G. Smith,* CAS
Treasurer: Dr. J. Wyatt Durham,*† UCB
Secretary: Dr. Ralph I. Smith,*† UCB
Dr. Donald P. Abbott,* SU
Crawford N. Cate,*† LACM
Dr. Ray Ghelardi,*† UCB; BML
Dr. Leo G. Hertlein,* CAS
Dr. A. Myra Keen,* SU
Dr. Robert C. Miller,* CAS
Dr. Frank A. Pitelka,*† UCB
Dr. Rudolf Stohler, Editor,* UCB

Members Elected Later, in Chronological Order

28 September 1965:	Dr. Charles Stasek,† UCB	Dr. Ray Ghelardi† resigned
16 September 1966:	Dr. Edmund Smith, Pacific Marine Sta.	
21 February 1967:		Charles Stasek† resigned
14 November 1968:	Dr. Victor Zullo, UCB	Dr. Robert Miller* resigned
5 August 1971:	Dr. Peter Rodda, CAS	Dr. Victor Zullo resigned
	Dr. James Valentine, UC, Davis	
	Dr. James Nybakken, Calif. State Univ., Hayward	
15 January 1972:		Dr. Leo Hertlein,* deceased
30 November 1972:	Dr. Warren O. Addicott, U.S. Geol. Survey	
17 August 1976:		Allyn Smith,* deceased
28 September 1977:	Dr. Carole Hickman,† UCB	
	Dr. David Phillips, UC, Davis	
17 November 1980:		Dr. James Nybakken resigned
9 August 1981:		Crawford Cate,*† deceased
30 July 1982:	Mrs. Jean Cate†	
1 April 1983:		Dr. Rudolf Stohler* resigned as Editor
21 April 1983:	Dr. David Lindberg, UCB	
	Dr. Terrence Gosliner, CAS	
25 September 1985:	Dr. Eugene Coan, CAS; LACM	
4 January 1986:		Dr. Myra Keen,* deceased
18 January 1986:		Dr. Donald Abbott,* deceased
28 September 1986:		Dr. Frank Pitelka*† resigned
4 May 1987:	Dr. James Carlton, UO	
	Dr. Barry Roth, CAS	
14 November 1988:	Dr. James Nybakken, Calif. State Univ., Hayward	

Current Executive Board (April 1989)

Jim Carlton, Jean Cate,† Eugene Coan (Treasurer), Wyatt Durham,*† Terry Gosliner (President), Cadet Hand,* Carole Hickman (Vice President), Dave Lindberg (Secretary), Jim Nybakken, David Phillips (Editor), Peter Rodda, Barry Roth, Ralph Smith*†

* Charter Member.
† Trustee.

receives donations. However, with *The Veliger* as our qualifying product, tax-deductible charitable donations became available to CMS, Inc., and are welcomed for either fund a donor may designate. Donations are gratefully received on a regular basis today, from both individuals and organizations.

Mail ballots were distributed among Board members, requesting approval for the corporation to borrow $7000, interest-free, from Dr. Stohler. The measure passed unanimously; the loan was made for basic funding of the new corporation. Transfers of funds and back issues of the journal were made from NCMC to CMS in June 1964.

With a few notable exceptions, CMS Executive Board meetings were about what one would expect—several triumphs, a few regrets, financial reports, occasional minor problems, and so on. Rather than outline 19 years' minutes of routine meetings, only those exceptions will be included here as they occur within the chronology of *The Veliger*'s story. Over the years, the original complement of 12 members diminished; some charter members resigned for positions elsewhere, and a few passed away. New members were gradually added as vacancies occurred (Table 1).

One of the early undertakings of the new Executive Board was its unanimous vote to publish a study done by undergraduate students at Hopkins Marine Station of Stanford University as the Supplement to Volume 6. The idea of one of our board members, Dr. Donald Abbott, it was an innovative, in-depth study of a single mollusk species, *Tegula funebralis* (A. Adams, 1855), with separate projects assigned to individual students along pre-planned guidelines. In a new way of studying marine biology, the resulting student papers were published in the supplement, encouraging young authors while providing a worthy, thorough study of a single species within a short time.

By this time, even Ruedi was more than fully occupied in producing bigger and better issues, plus several sizeable supplements. He was the only contact between authors and reviewers, as that connection was kept confidential. He also managed the banking, investments, and many other duties, while keeping abreast of current literature and writing many of the book reviews in every issue. As he now had a considerable work-overload, I was appointed to a second job as Business Manager, which entailed receiving payments, doing the bookkeeping, and handling general correspondence.

At a meeting in March 1965, a question was raised relative to obtaining a government grant to fund the cost of typesetting and illustrations. The same topic arose fairly frequently at Board meetings, but as Dr. Stohler was opposed to applying for grants to *The Veliger,* no action was taken; he preferred to have the journal earn its own way. By cutting costs wherever possible, it has always been self-sustaining. Although he did not disapprove of grants to individuals, he preferred to manage the journal on its own, and he paid the same annual dues as everyone else, to help toward that end.

Aside from frequent breakdowns of The Beast, there were never any important problems with production. The Beast remained at our house for 2 or 3 years, but always uppermost in Ruedi's mind was the need to move it to his own home, where he would have more time with his family; after all, he was still working full time for the University until his retirement there on 30 June 1969. However, he accumulated a great deal of uncompensated overtime through his special work as Zoology Department Collector and Research Zoologist, requiring him to range the entire coastline of California and into Baja California, Mexico, collecting marine animals—a job that kept him away from home a good deal of the time, often spending 70-hour work-weeks, many of them comprising 7 working days. He used this unpaid overtime and his 5 weeks' earned vacation for the quarterly typesetting stints.

He also used some of this "time off" to dig, by hand, an addition to the cellar beneath his house—a room measuring about 10.7 m L × 3 m W × 2.4 m H. Having no overhead space initially, he began by lying prone under the house and removing the soil, first with a hand trowel and bucket, later graduating to a short-handled shovel and wheelbarrow, and so on. He has said it required "a few months of spare time" to complete the job.

By early 1966 (Volume 9), the new cellar was ready to receive The Beast. Crawford had retired that year, and while we traveled to Australia and the South Pacific, Ruedi and Mrs. Genevieve Stohler stayed at our place for a time to supervise the partial dismantling of his clumsy "dinosaur" and other equipment for the move to Berkeley. The machine had to be maneuvered under our overhanging roof, then wrestled down a narrow stairway at the other end of the move. Despite its age, The Beast served Ruedi in a reasonably faithful manner for another 17 years.

In September of 1964, the Executive Board had approved publication of Winifred Arnold's glossary of malacological terms, and it appeared the following March as a supplement to Volume 7 (illustrated by Emily Reid). At the same meeting, the question of producing an index to *The Veliger* was brought up; it was explained that members of one of the shell clubs were already working on an index for the first 10 years of publication. This item dragged on, seemingly forever, with periodic reports that the index was "progressing nicely." In 1968 it was announced that the index to the first 10 volumes would be finished by the end of 1969. In 1981, we heard this news: "The Index to Volume 10 is complete!" It was also completely lost, as we soon discovered. After several months, half of it was found, totally unusable. We never learned exactly what had happened, but fortunately Dr. Stohler and others had already started planning a comprehensive Index to Volumes 1–25.

The first of several lively CMS Board discussions, over time, was held in 1966 as to the feasibility of publishing Dr. Joshua Baily's lifelong work on the mollusks of California, handwritten and contained in 50 thick looseleaf binders. The binders were kept in Baily's bank vault, and he was reluctant to lend even a few pages for a long enough period to allow an assessment of their value to malacology. He sincerely wanted it published in *The Veliger,* offering a generous amount of money toward that end. However, we feared that the work was by now so obsolete as to require a long, costly revision; we could not make any promises without first making a careful scientific appraisal of the material. Ruedi Stohler and I went to San Diego to discuss it further, but Baily was adamant about not allowing a single page out of the vault except for the purpose of publication. The hands of CMS were tied, without an opportunity for serious consideration as to whether it would be worth the time, effort, and expense that might be necessary to put it in order for publication. We could assess neither the work itself, nor whether the sum he had allotted would cover both its revision and publication costs. Nothing could be done.

While in session in 1967, we were asked by a visitor whether CMS, Inc. could conduct annual malacological conferences on the Pacific coast. Since producing the journal was our primary aim, and that was already as much as we could handle, no action was taken. The situation was eventually resolved by the independent formation of the Western Society of Malacologists (WSM) in 1969. The WSM brought new readers as well as new authors, among students eager to break into the realm of publishing. While of course they were not the primary source of articles in *The Veliger,* we felt it worthwhile to encourage promising young writers. Among authors who started early with *The Veliger* are Dr. Terrence Gosliner, Associate Curator and Department Head of the departments of Invertebrate Zoology and Geology at CAS, and now President of CMS, Inc., who at age 17 published his first scientific paper in

The Veliger (GOSLINER, 1968). Dr. Eugene Coan, now CMS Treasurer, at 19 also published his first paper within our pages (COAN, 1962). Both have since proved their value to malacology many times over.

On 20 May 1969, the most exciting board meeting of all never took place. A few of us assembled in our usual seminar room in LSB: President Cadet Hand, Allyn Smith, Ruedi Stohler, and I were there early, but no one else showed up. Owing to student riots on the Berkeley campus, the police had closed the grounds to all traffic in both directions. We soon realized that trouble was very near to us; students raged through the halls, loudly voicing their complaints. We locked the door, closed the curtain over its window, turned off the lights, and sat there in near darkness for over an hour, waiting out the siege. The mêlée was so close that police tear gas seeped in, leaving us coughing, wheezing, and with teary, red eyes.

Since LSB is a science laboratory building, there are emergency showers in the main halls outside each lab, in case of a chemical accident. The rioting students turned on every shower; the halls were an inch deep in water when we left the room. Lacking a quorum, President Cadet Hand adjourned the non-meeting when things quieted down, and we waded out, more subdued than the rioters. I recall being shocked to see bullet-proof vests for the first time that morning, when before starting their tours of duty, the well-prepared police crowded the coffee shop.

After more than 30 years' service, Ruedi Stohler retired officially from the University of California, Berkeley, in June 1969, but unlike many retirees, he had no problem finding ways to keep himself busy.

At a special meeting at Bodega Marine Laboratory in July 1970, it was announced that Dr. Stohler had donated two personal collections of rare stamps to CMS, Inc., and it was no surprise later to learn that the $6000 realized from their sale had been deposited in the Veliger Endowment Fund.

During 1970 (Volume 13), Crawford and I moved from Los Angeles to Sanibel Island, Florida. I created a small branch office in one end of a large utility room, and the long-distance move had little effect on tasks for *The Veliger*; we shipped the proofs by mail, with little delay in service. It was handled that way from then on; it was good to have our own library for references to check on the proofreading. In 1975 (Volume 17), we returned to California, this time to Rancho Santa Fé in San Diego County. In 1977, Crawford suffered a stroke, and was a semi-invalid until his death in 1981. I moved to a smaller home, and was glad to have my assorted duties to do for *The Veliger*.

In 1974, Dr. Donald Abbott proposed publication of another supplement, on the biology of chitons; this was approved by the Executive Board, and was published as a supplement to Volume 18. The Manager's report stated that earnings had remained the same as in the previous year, while expenses had decreased. Donations and memberships had dropped, but institutional subscriptions were slowly rising. The Glossary edition was sold out; the CMS debt to Dr. Stohler had now been paid in full within 10 years, and all money repaid on the loan had gone to Ruedi's favorite charity, The Veliger Endowment Fund.

Due to the narrowing of my peripheral vision from cataracts, the wide, 18-column bookkeeping ledger eventually became impossible to contend with, and in 1975 I resigned from the bookkeeping portion of the Manager's job. Fortunately, I could still read the proofs and continue handling dues, subscription payments, and general correspondence, so I remained as Manager except for coping with the big ledger. (Eye surgeries eventually brought everything back into focus.) But the bookkeeping still had to be done, so for the first CMS hired a part-time bookkeeper, our first paid staff member. We employed three different bookkeepers between 1975 and 1987, when that job was absorbed by Dr. Eugene Coan, the corporate Treasurer on the newly elected Executive Board of CMS.

In 1978, Ruedi purchased a computer for maintaining the journal's mailing list—a great improvement over clumsy Addressograph® plates—and to make address labels for the issues, which were now mailed in plastic sleeves. In 1982, he provided me with a computer as well, to compile certain portions of the index to Volumes 26–50 of *The Veliger*, that assignment having been approved by the Executive Board. My preparation of bibliographic, authors, and new taxa indices for the second half-century of publication continues today, along with proofreading the Trivial Names Index for Volumes 1–25.

In 1979 (Volume 22), we made another change in bookkeepers, and President Cadet Hand appointed me to the newly created position of Bursar, to verify vouchers, pay the bills, and provide quarterly accounting reports.

Based on the erroneous assumption that the long-awaited index to the first 10 volumes was now available, Ruedi proposed preparation of a cumulative index for the first 25 volumes, to be merged with the work supposed already done. His proposal was accepted by the Board at the annual meeting in July 1981.

Ruedi announced that owing to his failing vision, he would resign the editorship of *The Veliger* effective on completion of Volume 25(4), due 1 April 1983. At the same meeting, I was elected to the Executive Board as a Trustee.

In 1982, Board member Dr. David Phillips, having agreed to assume the new editorship, traveled to Lawrence, Kansas, to discuss arrangements with Allen Press, which specializes in publishing scientific journals. Following his report, it was agreed to contract with Allen Press for the printing of *The Veliger*, starting with Volume 26(1).

At that meeting, Dr. Stohler and I both voted for the first time as members of the Board. Though from the beginning he had attended all meetings as Editor and advisor, he had refused, on principle, to vote on his own suggestions.

The final issue under Ruedi's tenure, Volume 25(4) was

published in April 1983, with a total of 406 pages—more than 10 times the 40 pages of Volume 1. Other volumes had exceeded that size: for example, Volume 18 has 424 pages, plus a 128-page supplement. A bound set of the total 25-year work occupies more than a meter of shelf space and a grand total of 9362 pages—all produced by hand on either a typewriter or The Beast, a machine so outmoded that when Ruedi discontinued using it in 1983, workers were paid to dismantle it and haul it away as junk.

Dr. Stohler's day of resignation as Editor of *The Veliger* was officially 1 April 1983. It was the end of a memorable era. An excellent illustrated article about him by Dr. Ralph I. Smith was published in the first issue following Ruedi's retirement (*vide* SMITH, 1983).

* * * * *

Now the story of the first quarter-century of *The Veliger* and of the early years of CMS has been told. The facts are there, but it is impossible simply to come to a halt without making some attempt to express the spirit that lay beyond the bare facts of those years. However it may appear, that was far from being a time of difficult, drudging work; for me they were years of pleasure, learning new skills and disciplines, and feeling useful by helping to accomplish a worthwhile task. Ruedi Stohler made all this seem easy, and fun, and it was.

Few lives have been touched by Ruedi's *joie de vivre* and his ability to impart knowledge in a humorous way—the most effective form of teaching—without being enriched by the association. It would be difficult for anyone who was not there to imagine the pleasure we all had, working together to make *The Veliger* a superior journal, while *The Veliger*'s important work was done, too.

ACKNOWLEDGMENTS

I express gratitude to kind friends for their help in preparing this paper: Ruedi Stohler for refreshing my memory many times; Ralph Smith for keeping well-written minutes for some 30 years; Cadet Hand for a reminder about Dr. Hanna's color process; and Dave Lindberg for furnishing the three bulging binders of CMS minutes and a quiet space in which to work with them.

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Effects of Adult Suspension- and Deposit-Feeding Bivalves on Recruitment of Estuarine Infauna

by

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Abstract. A variety of theories, especially functional-group theories, have proposed that adult infauna may regulate community composition by affecting the survival or behavior of settling larvae and juveniles. The influence of adult suspension- and deposit-feeding bivalves (*Macoma balthica* and *Mya arenaria*) on infaunal recruitment was studied to observe the potential importance of such interactions. The two clams were transplanted at various densities into buckets of defaunated sediment during the spring of two years. Both species had generally similar effects on the densities of other fauna. Total macrofaunal abundance was reduced by both *Mya arenaria* and *Macoma balthica,* with the greatest decline occurring at highest clam densities. The densities of individual species were also affected, but the influence of the two clams varied among taxa and between years. The results suggest that *Macoma balthica* and *Mya arenaria* may alter community composition through a variety of direct and indirect effects upon recruitment. However, the pattern of effects is not consistent with that predicted by functional-group theories of faunal interactions in soft substrates. Indirect effects of the clams, resulting from their influence on one or two dominant taxa, may be more important on short time scales in determining the abundances of certain fauna.

INTRODUCTION

Recruitment success of infauna has been proposed as a potentially important process regulating the composition of soft-substrate benthic communities. Local hydrodynamic patterns, substrate characteristics, larval behavior, and predation by resident infauna may all act to determine larval settlement and subsequent survival (COMMITO, 1982; ECKMAN, 1983; WATZIN, 1983; WEINBERG, 1984; BUTMAN, 1986; WOODIN, 1986). Similarly, several functional-group hypotheses also have proposed that high densities of certain infauna may inhibit recruitment of organisms with specific ecological attributes. The adult-larval interaction hypothesis (WOODIN, 1976) suggests that discrete, dense assemblages of deposit feeders, tube dwellers, and suspension-feeding bivalves may be maintained through interactions between established adults and settling larvae or juveniles. Deposit feeders can ingest larvae in near-surface sediments or disrupt larvae and juveniles while searching for detrital food. Tube builders will pre-empt space otherwise available for settlement and can ingest larvae on the substrate surface. Suspension feeders can filter out planktonic larvae before they reach the bottom. The trophic-group amensalism hypothesis (RHOADS & YOUNG, 1970) predicts that deposit feeders can inhibit both adult and juvenile suspension feeders by resuspending large quantities of particulates, thereby clogging filtering appendages and organs. The mobility-mode hypothesis (BRENCHLEY, 1981, 1982) predicts that mobile species can prevent the establishment of sedentary organisms by destabilizing (often fluidizing) substrates and disrupting permanent tubes, burrows, or rhizome systems. Sedentary taxa, in turn, may bind sediments, inhibiting burrowing by mobile animals.

The actual importance of functional-group interactions to settlement patterns and community composition has been debated. Recruitment may be affected by a wide variety of physical and biological factors that may overwhelm functional-group effects (COMMITO, 1982; ECKMAN, 1983; BUTMAN, 1986). Substrate characteristics are well known

to be correlated with faunal distributions (Allen, 1899; Peterson, 1913; Sanders, 1956, 1958) and the influence of wave and tidal disturbance of sediments can be many times that due to biogenic reworking (Grant, 1983). Small variations in hydrodynamic regimes can also have a significant effect on the ability of larvae to settle (Butman, 1986; Butman *et al.*, 1988). Predation may strongly affect survivorship of infauna (Peterson, 1979, 1982), while the intensity and impact of biological activities, such as suspension feeding, bioturbation, or deposit feeding, may depend upon species characteristics or overall faunal densities (Hunt *et al.*, 1987; Posey, 1987).

Despite the influence of these other factors, several studies have suggested that functional-group interactions between adult infauna and recruits can alter the local species composition of benthic communities. An important area of research in benthic ecology is to determine if and when such interactions become a dominant factor in structuring these habitats. The present study examines the effects of two infaunal bivalves, the suspension-feeding *Mya arenaria* L. and the deposit-feeding *Macoma balthica* L., on recruitment of other species. This study has three primary objectives: (1) determine whether varying the densities of these large and trophically different species can affect recruitment and short-term community development, (2) if so, observe whether their effects are consistent with the predictions of functional-group hypotheses, and (3) observe whether effects may vary annually with variations in settlement intensity.

The soft-shell clam, *Mya arenaria,* and the balthic clam, *Macoma balthica,* are common inhabitants of intertidal and shallow subtidal fine sands along both the Atlantic and Pacific coasts of North America. *Mya arenaria* is a deep-burrowing, sedentary suspension feeder (Purchon, 1968) while *Macoma balthica* is a deep-burrowing, surface deposit feeder that may facultatively suspension feed under restricted conditions (Brafield & Newell, 1961; Maurer, 1967). *Macoma balthica* can produce a fluid, fecal-rich layer on the sediment surface as a result of its feeding activities (Rhoads & Young, 1970; Risk & Moffat, 1977).

Both *Mya arenaria* and *Macoma balthica* may be expected to regulate community composition by affecting patterns of faunal recruitment. Functional-group hypotheses predict that a suspension-feeding bivalve, such as *Mya arenaria,* will negatively affect the recruitment of species with small planktonic larvae by removing them before they reach the substrate surface (adult-larval interactions; Woodin, 1976). Several studies have indicated that suspension feeders may remove significant quantities of particulates and larvae from the water column (Breese & Phibbs, 1972; Mileikovsky, 1974; Peterson, 1979; Williams, 1980; Frithsen & Doering, 1986). Surface deposit feeders, such as *Macoma balthica,* may ingest or disrupt surface-dwelling taxa whose larvae do not possess a depth refuge from their feeding activities (adult-larval interactions; Woodin, 1976), prevent the establishment of sedentary species that are subject to bioturbation (mobility-mode interactions; Brenchley, 1981; Posey, 1987), or inhibit feeding by suspension-feeding taxa through increased resuspension of sediments (trophic-group amensalism; Rhoads & Young, 1970; Aller & Dodge, 1974).

MATERIALS AND METHODS

The effects of *Macoma balthica* and *Mya arenaria* on community development were examined using transplants near the mouth of the Rhode River, Maryland, in the lower mesohaline zone of the western shore of the Chesapeake Bay (36°51′N, 78°32′W; see Hines & Comtois, 1985, for description). Salinities range from a spring low of 4–7‰ to a high of 11–15‰ in late summer and fall (Hines & Comtois, 1985; Hines *et al.*, 1987). Most recruitment into the infaunal community occurs in the spring from March through May. Infaunal densities decline sharply in summer, apparently in response to a seasonal increase in the densities of predatory fish and crabs (Virnstein, 1977; Holland *et al.*, 1980; Hines *et al.*, 1987).

To examine the influence of *Mya arenaria* and *Macoma balthica* on this recruitment, both species were planted separately into buckets of defaunated sediment during the spring of 1981 and 1982. Sediment from an area adjacent to the experimental site was collected in December 1980 and 1981 and subsequently placed in buckets on shore to freeze during winter. Collecting fresh sediment each year increased similarity between buckets and ambient sediments, reflecting natural fluctuations in sediment composition that may occur over the course of a year. Immediately prior to the start of each experiment in March, the frozen and thawed sediment was pooled into a large tub and thoroughly mixed. The sediment was then seived through a 7-mm screen to remove large shells and large dead clams and was then placed into plastic buckets (0.06 m^2 surface area × 35 cm deep). Examination of the sediment under a dissecting microscope confirmed the lack of living macrofauna and meiofauna at the start of experiments. Sediments used during the two years were similar, consisted of 35% silt and clay, 50% fine to medium sand (80–500 μm), and 15% coarse sand (>500 μm).

The buckets of sediment were assigned to five treatments: (1) zero clams, $n = 7$ in 1981 and $n = 10$ in 1982; (2) high *Mya arenaria* density (50 live clams per bucket), $n = 6$ in 1981 and $n = 10$ in 1982; (3) low *Mya arenaria* density (12 clams), $n = 6$ in 1981 and $n = 10$ in 1982; (4) high *Macoma balthica* density (50 clams), $n = 5$ in 1981 and $n = 10$ in 1982; and (5) low *Macoma balthica* density (12 clams), $n = 5$ in 1981 and $n = 10$ in 1982. Low density treatments for both clams approximate natural densities in the Rhode River (Hines & Comtois, 1985). High density treatments are within the range of high densities reported for these species by other authors (Rhoads & Young, 1970; Olafsson, 1986; Emerson *et al.*, 1988). *Mya arenaria* was obtained from local commercial fishermen operating escalator dredges near the mouth of the

Rhode River, while *Macoma balthica* was collected from hand-operated box cores in the Rhode River. *Mya arenaria* is a larger species than *Macoma balthica* and this natural size difference was reflected in the individuals used in this experiment (mean *Mya arenaria* shell length: 65.5 ± 7.5 mm; mean *Macoma balthica* shell length: 27.6 ± 2.3 mm).

Clams were held in the laboratory for one day to observe any damage or mortality associated with collection. Live, undamaged individuals were placed into the buckets of sediment with water at the previously described densities and were left until they had burrowed. The buckets were placed on the bottom in 2.5 m of water on 10 March 1981 and on 19 March 1982. All buckets were retrieved on 18 May 1981 and 25 May 1982, respectively. Placement of buckets on the substrate surface was necessitated by the difficulty in burying up to 50 buckets at a time flush with the sediment surface, using SCUBA, and later attempting to recover them in turbid waters. Although the placement of the buckets on, and not dug into, the sediment may affect hydrodynamic characteristics and possibly settlement patterns (Eckman, 1983; Butman, 1986), this was not considered a problem in analysis since all comparisons were made between buckets treated in the same manner. However, to observe whether such a placement and the use of defaunated sediments produced significantly different patterns than seen in the ambient community, core samples (0.01 m^2 × 35 cm deep) from adjacent areas were compared with the zero clam-density bucket samples.

The macrofauna in each bucket at the end of 1981 experiments was sampled by seiving the entire bucket of sediment through a 0.5-mm mesh. However, this methodology proved time consuming and, in order to increase replication of buckets, the 1982 experiments were sampled by taking a central core of sediment (0.01 m^2 × 35 cm deep) from each bucket and then seiving the contents of the core on a 0.5-mm screen. Separate comparisons of faunal density estimates from the two methods, involving the application of both techniques to 10 buckets, indicated that they provide indistinguishable results for all but rare taxa ($P > 0.09$, paired t-tests for the 12 most abundant taxa). Counts for the 1981 and 1982 experiments were adjusted for a constant area before statistical analyses. All organisms retained on a 0.5-mm seive were fixed in 10% formalin solution, stained with rose bengal dye, and identified to species with the aid of a dissecting microscope.

Faunal densities were compared among treatments using three-way analysis of variance. The statistical tests examined the effects of clam density (zero, low, high), clam species (*Mya, Macoma*), year (1981, 1982), and interactions between these variables on total faunal abundances as well as the densities of numerically dominant taxa. Data were log-transformed before analysis and a F_{max} test (Sokal & Rohlf, 1981) indicated homogeneity of variances after transformations. For statistical analyses, the zero-density control buckets were randomly assigned as control treatments for either the *Mya arenaria* or *Macoma balthica* experiments (4 in 1981 and 5 in 1982 as zero-density *Macoma balthica*, 3 in 1981 and 5 in 1982 as zero-density *Mya arenaria*).

RESULTS

Most *Mya arenaria* and *Macoma balthica* placed within the buckets survived until the end of experiments. For 1981, percent survivorships (with the mean ± SD number of clams in parentheses) for each treatment were: high-density *Mya* = 87% (44.3 ± 3.4); low-density *Mya* = 90% (10.8 ± 4.7); high-density *Macoma* = 84% (41.8 ± 3.9); and low-density *Macoma* = 82% (9.8 ± 0.9). For 1982, the percent survivorship of clams was: high-density *Mya* = 95% (47.3 ± 2.6); low-density *Mya* = 92% (11.0 ± 0.9); high-density *Macoma* = 86% (43.0 ± 3.7); and low-density *Macoma* = 97% (11.6 ± 0.4). The surviving clams all appeared healthy at the end of experiments.

The placement of buckets of defaunated sediment on the substrate surface did not produce dramatically different patterns of abundance compared to surrounding areas. Comparison of total macrofaunal densities within the control buckets at the end of experiments compared to an adjacent area showed no significant difference during 1981 ($\bar{x}$ in buckets = 7666.5 animals/m^2 [SE = 2277.2], $\bar{x}$ outside buckets = 8881.2/m^2 [SE = 2542.5]; $F = 0.21$, $P > 0.65$), though there were higher densities within buckets during 1982 ($\bar{x}$ in buckets = 1484.6 animals/m^2 [SE = 106.4], $\bar{x}$ outside buckets = 733.22/m^2 [SE = 77.1]; $F = 28.62$, $P < 0.001$). During both years, the majority of common species (see below) showed no difference in abundance between control buckets and adjacent areas ($P > 0.05$; 7 of 12 species during 1981, 8 of 12 species during 1982). Given an expectation of some differences in abundance between a community developing from defaunated conditions and one that had not been defaunated, these results suggest minimal artifacts due to experimental design.

A three-way analysis of variance (ANOVA) indicated significant effects of clam species (*Mya* vs. *Macoma*), clam density, and year of experiment on total macrofaunal abundance (Table 1). Varying the densities of both *Mya arenaria* and *Macoma balthica* had qualitatively similar effects on total densities, with lower numbers of other macrofauna being associated with high densities of both clam species (Figure 1). There was a marked decline of recruitment into the buckets from 1981 to 1982, as indicated by highly significant variations in total macrofaunal density between years. Such annual variability in recruitment is well documented from temperate estuaries (Flint & Younk, 1983; Dauer, 1984; Hines et al., 1987; Posey, 1986; Holland *et al.*, 1987). The density effects of both *Mya arenaria* and *Macoma balthica* on total faunal abundances persisted despite these fluctuations in recruitment between years. In addition to significant treatment effects, interactions were significant between clam density and both year and clam species. However, these interactive terms were small relative to the main effects (as indicated by F-ratios, Table 1).

Table 1

Influence of clam species (*Macoma* vs. *Mya*), clam density (0, 12, or 50 per 0.06 m^2), and annual variability on macrofaunal abundance. Values are *F*-ratios from a three-way analysis of variance.

	Main effects			Interaction terms			
Taxa	Clam species	Clam density	Year	Species* density	Species* year	Density* year	Species* density* year
Bivalvia							
Macoma balthica	0.4^{ns}	3.17*	0.03^{ns}	6.73**	4.25*	6.15**	0.56^{ns}
Macoma mitchelli	0.05^{ns}	0.40^{ns}	0.08^{ns}	1.38^{ns}	0.68^{ns}	2.42^{ns}	1.13^{ns}
Mya arenaria	7.94**	10.50****	313.13****	2.46^{ns}	3.93^{ns}	16.02****	1.25^{ns}
Polychaeta							
Heteromastus filiformis	0.22^{ns}	12.47****	21.87****	4.37*	5.86*	4.85*	3.01^{ns}
Eteone heteropoda	0.01^{ns}	0.54^{ns}	25.40****	1.91^{ns}	3.91^{ns}	0.37^{ns}	1.37^{ns}
Nereis succinea	3.38^{ns}	1.09^{ns}	30.83****	0.16^{ns}	6.59*	0.27^{ns}	6.71**
Polydora ligni	0.04^{ns}	7.47**	300.29****	8.63***	2.71^{ns}	4.37*	0.39^{ns}
Scolecolepides viridis	8.63**	6.42**	215.79****	5.76**	4.76*	12.99****	0.64^{ns}
Streblospio benedicti	0.36^{ns}	0.28^{ns}	25.81****	1.71^{ns}	1.03^{ns}	5.75**	6.75**
Crustacea							
Cyathura polita	7.79**	7.50**	198.90****	10.72****	7.79**	7.50**	10.72****
Corophium lacustre	9.14**	39.73****	132.88****	3.05^{ns}	0.01^{ns}	1.20^{ns}	1.53^{ns}
Leptocheirus plumulosus	0.01^{ns}	1.57^{ns}	2.28^{ns}	0.01^{ns}	1.64^{ns}	2.47^{ns}	0.96^{ns}
Total macrofauna	10.37**	52.60****	320.87****	5.29**	0.70^{ns}	3.19*	2.01^{ns}

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$.

Twenty-two species constituted the macrofauna in the experimental buckets during the two years. However, only 12 species had mean densities per bucket that were significantly greater than zero for two or more treatments (Students *t*-tests, $P < 0.05$); and only the densities of these common species were compared among treatments. These species included a variety of taxa (polychaetes, crustaceans, and bivalves) as well as a variety of trophic, mobility, and developmental patterns (Table 2). All 12 species are dominant members of the naturally established infaunal communities of the Rhode River (Hines & Comtois, 1985; Hines *et al.*, 1987). None of the species that occurred in the buckets but were not considered in the analyses had a mean density greater than four individuals per bucket in any treatment.

The densities of seven of these 12 common species were affected by variations in clam density and four showed differences in recruitment between the two clam species (Table 1). Nine species also displayed highly significant variations in abundance between the two years (Table 1). However, interactions were numerous among these main effects, making interpretation of their overall importance difficult. Because of these strong interactions, the influence of varying clam density on macrofaunal abundance was examined separately for each clam species during each year (one-way ANOVA).

As introduced before, several functional-group hypotheses make specific predictions about the effects of both surface deposit feeders, such as *Macoma balthica,* and suspension feeders, such as *Mya arenaria,* on the abundances of species with particular trophic and mobility characteristics (Table 2). Both *Mya arenaria* and *Macoma balthica* had qualitatively similar effects on faunal abundances during 1981 (Figure 2; Table 3). Four species exhibited a pattern of higher abundance with low densities of one or both clam species, while four other species were negatively associated with increasing clam density. *Macoma balthica* recruits were most abundant in buckets containing low densities of *Macoma balthica* and low or high densities of *Mya arenaria.* Similarly, *Heteromastus filiformis* reached highest densities with low density *Macoma balthica* treatments, and *Mya arenaria* recruits were more abundant with low densities of *Mya arenaria* adults (a similar, though non-significant, trend occurred for *Mya arenaria* recruits in low-density *M. balthica* treatments [Figure 2]). This pattern of highest densities with low clam abundance was also exhibited by a tube-dwelling spionid polychaete, *Scolecolepides viridis,* with *Macoma balthica. Polydora ligni* and *Corophium lacustre* were negatively associated with increasing clam density. Both species had significantly lower densities with high densities of *Mya arenaria* and *Macoma balthica* compared to clam absence. Neither displayed a trend towards highest densities with low abundances of either clam species. Two free-burrowing species were also negatively associated with increased clam density (*Nereis succinea* with *Macoma balthica* and *Cyathura polita* with *Mya arenaria*). A ninth species, *Streblospio benedicti,* exhibited only a marginally significant response to varying *Mya arenaria* abundance.

In 1982, macrofaunal densities within the buckets were much lower than observed in 1981, reflecting lower recruitment in the Rhode River during this second year of

Table 2

Ecological attributes of principal species in the Rhode River community and predicted effects of clam abundance from functional group hypotheses. References for attributes in parentheses: 1 = Brafield & Newell, 1961; 2 = Maurer, 1967; 3 = Rhoads & Young, 1970; 4 = Reinharz & O'Connell, 1981; 5 = Thorson, 1946; 6 = Hines & Comtois, 1985; 7 = Purchon, 1968; 8 = Chanley & Andrews, 1971; 9 = Dauer *et al.*, 1981; 10 = Fauchald & Jumars, 1979; 11 = Blake, 1969; 12 = George, 1966; 13 = Dean, 1965; 14 = Rasmusson, 1956; 15 = Banse, 1954; 16 = Bousfield, 1973; 17 = Burbanck, 1967; 18 = Hines, personal observations.

Taxa	Adult feeding mode	Tube or burrow construction	Reproductive mode	Vertical location in sediment		Predicted effects of bivalves	
				Juvenile	Adult	*Macoma*	*Mya*
Bivalvia							
Macoma baltica (1, 2, 3, 4, 5, 6, 18)	Surface deposit/ facultative suspension	No	Planktonic larvae	Surface	Deep	neg.[b]	neg.[b]
Macoma mitchelli (1, 2, 3, 4, 6, 9, 18)	Surface deposit/ facultative suspension	No	Planktonic larvae	Surface	Subsurface	neg.[b]	neg.[b]
Mya arenaria (3, 4, 6, 7, 8, 18)	Suspension	Semi-permanent tube for siphon	Planktonic larvae	Surface	Deep	neg.[a,b,c]	neg.[b]
Polychaeta							
Heteromastus filiformis (4, 6, 12, 14, 18)	Subsurface deposit	Mucous-lined burrow	Brooding planktonic larvae	Deep	Deep	0	neg.[b]
Eteone heteropoda (6, 12, 14, 18)	Surface predator	No	Planktonic larvae	Surface	Surface	neg.[b]	neg.[b]
Nereis succinea (4, 6, 12, 14, 15, 18)	Surface predator	Mucous-lined burrow	Planktonic larvae	Surface	Deep	neg.[b]	neg.[b]
Polydora ligni (5, 6, 9, 12, 11, 18)	Surface deposit/ facultative suspension	Horizontal tube	Brooding planktonic larvae	Surface	Surface	neg.[b,c]	neg.[b]
Scolecolepides viridis (5, 6, 9, 10, 12, 18)	Surface deposit	Vertical tube	Planktonic larvae	Surface	Subsurface	neg.[b,c]	neg.[b]
Streblospio benedicti (6, 9, 10, 13, 18)	Surface deposit/ facultative suspension	Horizontal tube	Brooding planktonic larvae	Surface	Surface	neg.[b,c]	neg.[b]
Crustacea:							
Cyathura polita (6, 17, 18)	Subsurface deposit	Unlined burrow	Brooding	Subsurface	Subsurface	0	0
Corophium lacustre (6, 16, 18)	Surface deposit/ suspension	Horizontal tube	Brooding	Surface	Surface	neg.[b,c]	0
Leptocheirus plumulosus (6, 16, 18)	Surface deposit/ scavenger	Horizontal tube	Brooding	Surface	Surface	neg.[b,c]	0

[a], trophic-group amensalism (Rhoads & Young, 1970); [b], adult-larval interactions (Woodin, 1976); [c], mobility-mode interactions (Brenchley, 1981, 1982).

experiments (Figure 1; Hines *et al.*, 1987). The number of species affected by increasing clam density was also less in 1982. One species, *Corophium lacustre,* was less abundant with increasing densities of both *Mya arenaria* and *Macoma balthica,* a pattern similar to that seen for this species in 1981. Another species (*Heteromastus filiformis*) was most abundant with low *Macoma balthica* densities but exhibited only marginally significant responses to *Mya arenaria.* Three other species (*Polydora ligni, Scolecolepides viridis,* and *Streblospio benedicti*) were significantly affected only by varying densities of *Macoma balthica,* all three having lower abundances with higher *Macoma balthica* densities relative to clam absence (Figure 3). Only one species, *Scolecolepides viridis,* showed a qualitatively different response to clam density from 1981 to 1982. This spionid polychaete reached highest numbers with low-density *Macoma balthica* treatments in 1981, but was negatively associated with this clam in 1982. Total faunal abundances were lowest with high densities of both species during both 1981 and 1982 (Table 3; Figure 1).

DISCUSSION

Both *Mya arenaria* and *Macoma balthica* had major effects on recruitment and benthic community composition in the Rhode River. Total faunal abundances were reduced by both species during both years of experimentation, with highest clam densities having the strongest effect on faunal

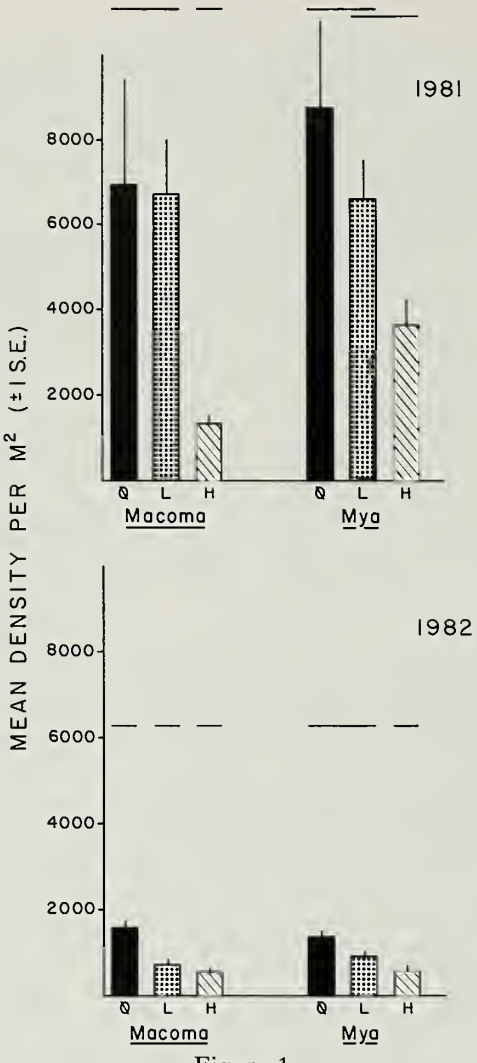

Figure 1

Influence of varying *Macoma balthica* and *Mya arenaria* densities on total macrofaunal abundances in 1981 and 1982. 0, no clams; L, 12 clams/0.06 m²; H, 50 clams/0.06 m². Means connected by lines are not significantly different (Scheffé's tests, calculated separately for both *Macoma* and *Mya*).

densities. However, the impact of these clams varied among infaunal species as well as between years. During 1981 there were two general forms of density change associated with increasing clam density: (1) a positive association of certain species with intermediate clam density, and (2) a negative association of certain other species, as well as total faunal abundance, with clam presence. Similarly, overall effects varied between years. Only about one-half of the species responding to varying clam density in 1981 were affected by either *Mya arenaria* or *Macoma balthica* in 1982. Part of this difference between years may reflect the dramatic differences in overall recruitment. Faunal densities within the buckets and in natural surrounding sediments were almost an order of magnitude lower in 1982 than in 1981. Density-dependent inhibition or enhancement of recruitment (as proposed by functional-group and competition hypotheses) may become proportionately less intense with lower juvenile abundance.

The variability between years and the variation of effects among species may also be in response to indirect effects of clam presence. The macrofauna in zero-clam treatments in 1981 were dominated by two tube-dwelling species, *Corophium lacustre* and *Polydora ligni*. Both of these species were strongly reduced in the presence of *Mya arenaria* and *Macoma balthica*. However, both *Corophium* spp. and *Polydora ligni* have been shown to aggressively exclude certain polychaetes and tube-dwelling crustaceans, including small, near-surface fauna similar to those affected in this study (Levin, 1982; Gallagher et al., 1983; Wilson, 1983). Part of the enhancement in faunal densities associated with low densities of the two clams may be in response to the reduction of these aggressive species rather than to direct enhancement by the clams. Reduction of *Polydora* and *Corophium* populations may be the result of disruption to their tube mats from bivalve feeding activities or burrow maintenance (Rhoads & Young, 1970; Posey, 1987).

Although not tested directly in this study, enhancement of macrofauna only at intermediate clam densities may occur if high densities of these bivalves have a detrimental effect that obscures indirect enhancement due to reduction of a dominant species. Such enhancement at intermediate densities of a disturber or predator has been noted in other systems with competitive dominants (Paine, 1974; Menge *et al.*, 1986). The possibility that inhibition of *Corophium* and *Polydora* may benefit other fauna is supported by the general lack of macrofaunal enhancement at low clam densities in 1982, when recruitment of both *Corophium* and *Polydora* was greatly lowered. In contrast, species that were negatively associated with both high and low densities of *Macoma balthica* and *Mya arenaria* in 1981 were also negatively associated with these species in 1982. Thus, the two bivalves may affect faunal abundances both directly and indirectly. In particular, disruption of tube mats, as associated with *Polydora* and *Corophium*, may enhance abundances of species that otherwise might be inhibited by these organisms, while other species may be directly inhibited by *Macoma balthica* or *Mya arenaria* burrowing or feeding activities.

The results of this study demonstrate the importance of adult infauna in regulating recruitment into a benthic community; however, they fail to support functional approaches to understanding these interactions. At least during the first year of experiments, *Mya arenaria* and *Macoma balthica* had generally similar effects on the abundances of other fauna. This similarity occurred despite the different feeding modes of the species and the different effects of these two species that are predicted from various functional-group hypotheses. For example, the suspension-feeding *Mya arenaria* is predicted to affect negatively species that have planktonic larvae but to have less of an effect on species that brood their young (adult-larval interaction

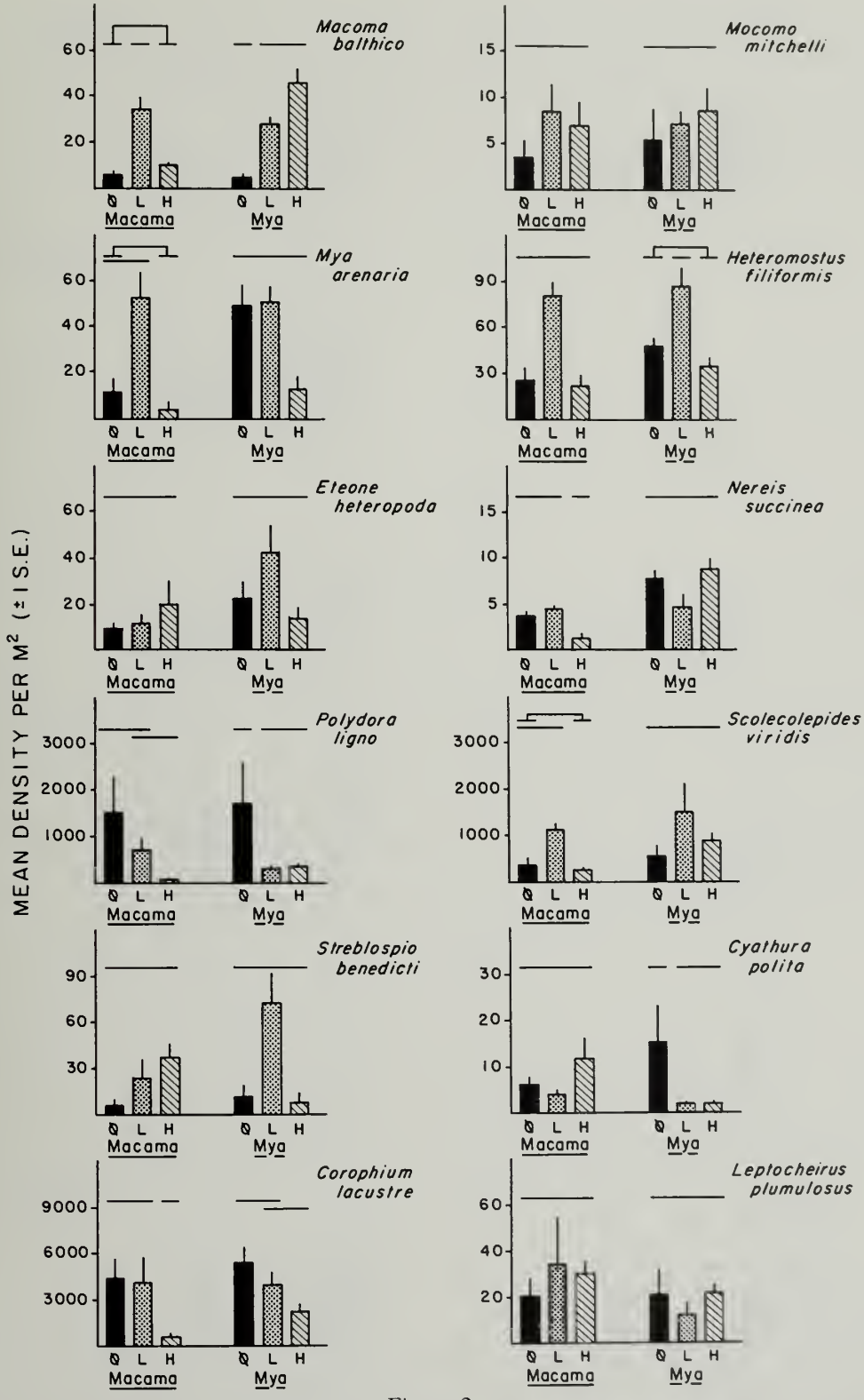

Figure 2

Influence of varying *Macoma balthica* and *Mya arenaria* densities on common macrofauna during 1981. 0, no clams; L, 12 clams/0.06 m²; H, 50 clams/0.06 m². Means connected by lines are not significantly different (Scheffé's tests, calculated separately for both *Macoma* and *Mya*).

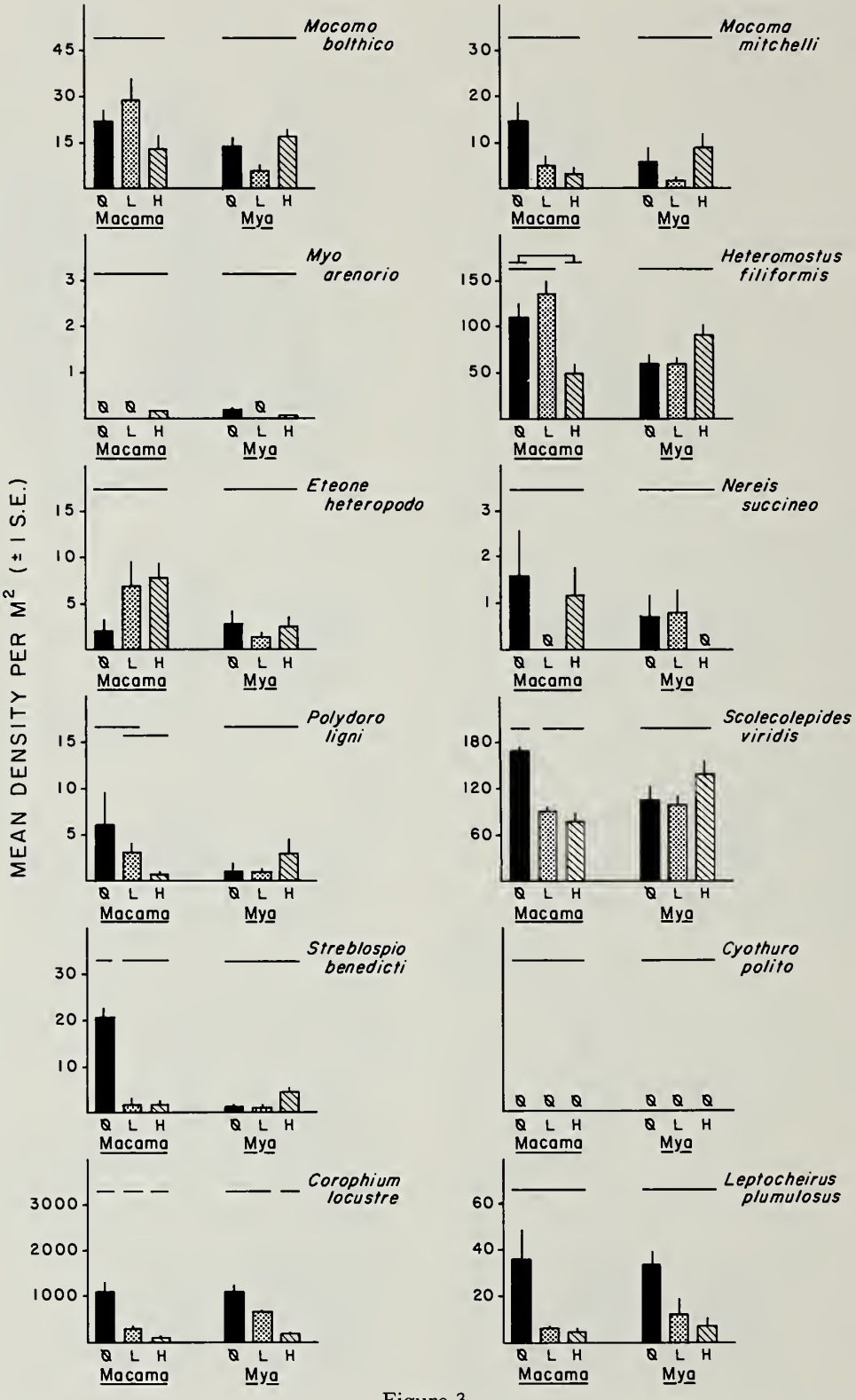

Figure 3

Influence of varying *Macoma balthica* and *Mya arenaria* densities on common macrofauna during 1982. 0, no clams; L, 12 clams/0.06 m²; H, 50 clams/0.06 m². Means connected by lines are not significantly different (Scheffé's tests, calculated separately for both *Macoma* and *Mya*).

Table 3

Influence of varying densities of *Macoma balthica* and *Mya arenaria* on the abundances of common macrofauna. Values are *F*-ratios from a one-way analysis of variance.

Taxa	1981		1982	
	Macoma	*Mya*	*Macoma*	*Mya*
Bivalvia				
Macoma balthica	18.30***	11.73**	1.44^{ns}	2.63^{ns}
Macoma mitchelli	0.67^{ns}	0.27^{ns}	2.68^{ns}	2.65^{ns}
Mya arenaria	6.29*	4.90*	0.73^{ns}	0.91^{ns}
Polychaeta				
Heteromastus filiformis	4.48*	14.95***	6.07**	3.85*
Eteone heteropoda	0.59^{ns}	1.70^{ns}	1.86^{ns}	0.28^{ns}
Nereis succinea	9.36**	1.40^{ns}	2.14^{ns}	1.58^{ns}
Polydora ligni	6.11*	4.26*	4.40*	2.01^{ns}
Scolecolepides viridis	5.37*	2.49^{ns}	5.30*	2.81^{ns}
Streblospio benedicti	2.06^{ns}	4.30*	7.01**	1.63^{ns}
Crustacea				
Cyathura polita	1.73^{ns}	7.31**	—[a]	—[a]
Corophium lacustre	9.58**	5.58*	17.77****	11.86***
Leptocheirus plumulosus	0.17^{ns}	0.45^{ns}	3.26^{ns}	2.06^{ns}
Total macrofauna	11.35**	5.82*	29.59****	11.25***

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$; [a], absent.

hypothesis; Woodin, 1976). In this study, *Mya arenaria* at low densities enhanced the densities of certain species with planktonic larvae (*e.g., Macoma balthica* and *Heteromastus filiformis*) while high densities of this bivalve negatively affected organisms that brood their young (*e.g., Corophium lacustre*). *Macoma balthica* is predicted to affect negatively suspension-feeding species (trophic-group amensalism; Rhoads & Young, 1970), species with non-burrowing larvae (adult-larval interaction hypothesis; Woodin, 1976), and sedentary species (mobility-mode hypothesis; Brenchley, 1981, 1982). Some members of all three groups were enhanced at low densities of *Macoma balthica* while others were negatively associated with this clam. Both clams appeared to have a variety of effects on functionally similar species. For example, both species negatively affected certain tube builders, such as *Corophium lacustre* and *Polydora ligni,* but were positively associated with other tube dwellers, such as *Streblospio benedicti.* Thus, predictions based solely on a species trophic type or mobility mode do not explain adequately the effects of these bivalves on recruitment.

These results join a growing literature emphasizing caution in the use of functional approaches to benthic communities. Several studies have shown that functional-group interactions may be important under certain circumstances, usually involving large, active, burrowing species (Aller & Dodge, 1974; Ronan, 1975; Peterson, 1977, 1984; Bird, 1982; Posey, 1986, 1987). However, the importance of these density-dependent group effects may vary depending upon the relative sizes of the interacting species (Wilson, 1981; Peterson, 1984; DeWitt & Levinton, 1985), activity rates (Wilson, 1984; Posey, 1987), or life-history characteristics (Weinberg & Whitlatch, 1983). In this study, *Mya arenaria* and *Macoma balthica* were predicted to have specific effects on other macrofauna. In actuality, their effects varied, some consistent with functional-group hypotheses and some not. Many of these inconsistencies may be related to the relative sizes or activity of the species involved as well as to indirect effects resulting from the reduction of aggressive or dominant species. This study emphasizes the growing consensus that functional-group approaches must be viewed with caution and may apply primarily under restricted conditions involving large or functionally dominant organisms.

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Oystercatcher Predation and Limpet Mortality: The Importance of Refuges in Enhancing the Reproductive Output of Prey Populations

by

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Abstract. On the rocky shores of seabird-breeding islands in Saldanha Bay, South Africa, the limpet *Patella granularis* is preyed upon by African black oystercatchers, *Haematopus moquini*. Limpets escape predation as a consequence both of the development of foliose algae on their shells, and of their rapid growth rate which results in their growing too large for oystercatchers to handle efficiently. Both these factors significantly enhance the probability of limpet survival. Although these means of escaping predation probably are coincidental and not evolved adaptations, they may contribute to the persistence of the limpet population through the reproductive output by large and fecund individuals. On adjacent mainland shores, where limpet and algal production rates are slow, oystercatchers are all but absent from the intertidal system.

INTRODUCTION

Birds are important predators in many intertidal communities and their removal of large numbers of prey items (GIBB, 1956; FEARE, 1966; BAIRD *et al.*, 1985) may result in severe depletion of the food resource (FEARE, 1969; O'CONNOR & BROWN, 1977; GOSS-CUSTARD, 1980; GOSS-CUSTARD *et al.*, 1980; FRANK, 1982). In addition, the preference of avian predators for certain prey size classes and morphotypes may modify prey population demography and reproductive output (GIESEL, 1970; HARTWICK, 1981; HOCKEY & BRANCH, 1983, 1984; BRANCH, 1985; LINDBERG *et al.*, 1987; MARSH, 1987).

In some instances intense avian predation on populations of rocky intertidal invertebrates has contributed to the evolution of adaptations that enable prey to escape detection and capture. For example, in some areas, the intertidal limpet *Lottia digitalis* (Rathke, 1833) (=*Collisella digitalis*) actively seeks vertical and overhanging rock faces, inaccessible to avian predators, on which to attach in the presence of American black oystercatchers, *Haematopus bachmani* (Audubon, 1838) (HAVEN, 1971; HAHN, 1985). The activity patterns of *Lottia limatula* (Carpenter, 1864) (=*Collisella limatula*) and *Collisella scabra* (Gould, 1846), and the homing behavior of many species of gastropods, have been shown to enhance survival in the face of predation (WELLS, 1980; GARRITY & LEVINGS, 1983). In addition, many intertidal prey organisms are cryptic and avoid detection by virtue of homochromy with the substratum (MERCURIO *et al.*, 1985), or mimicry of a common but inedible species (HOCKEY *et al.*, 1987).

Prey organisms may also escape predation by having refuges in space and size. Although not necessarily evolved adaptations, these means of escape may have a significant impact on prey population dynamics (TAYLOR, 1984). On the rocky shores of seabird-breeding islands in Saldanha Bay, South Africa, African black oystercatchers, *Haemat-*

opus moquini (Bonaparte, 1856), occur at some of the highest densities recorded (Hockey, 1983). At the three major islands in the Bay (Malgas, Jutten, and Marcus islands) the densities range from 25 to 78 birds per km of coast. Intertidal limpets are important prey of these resident, territorial predators (Hockey & Underhill, 1984), and their estimated annual removal of *Patella granularis* (L., 1758) from the shores of Jutten Island is 1.1 million individuals per km of coast (Hockey & Branch, 1984).

However, because oystercatchers prefer limpets of between 20 and 40 mm in length (Hockey & Underhill, 1984), larger limpets have a refuge from predation. In addition, some limpets inevitably settle in, or move to, positions that render them inaccessible to oystercatchers (*e.g.*, on vertical rock faces or the sides of crevices), thus attaining a refuge in space. The shores of seabird-breeding islands in Saldanha Bay support numerous foliose algae, which have a rapid rate of production in response to nutrient enrichment of intertidal waters by the dissolved guano of seabirds (Bosman & Hockey, 1986). Foliose algae also develop on the shells of *Patella granularis* which may, as a consequence, be totally hidden from view. This crypticity, although transient and not genotypic in origin, may be expected to enhance limpet survival in the presence of visually hunting predators.

In this study we assess the roles played by crypticity and refuges in size and space in enhancing the survival of limpets at sites with different levels of predatory pressure. None of these means of escaping predation necessarily represents an evolved adaptation and any influence on limpet survival rates may be merely coincidental. However, the escape from predation of certain elements of the prey population has potential long-term implications for prey population dynamics.

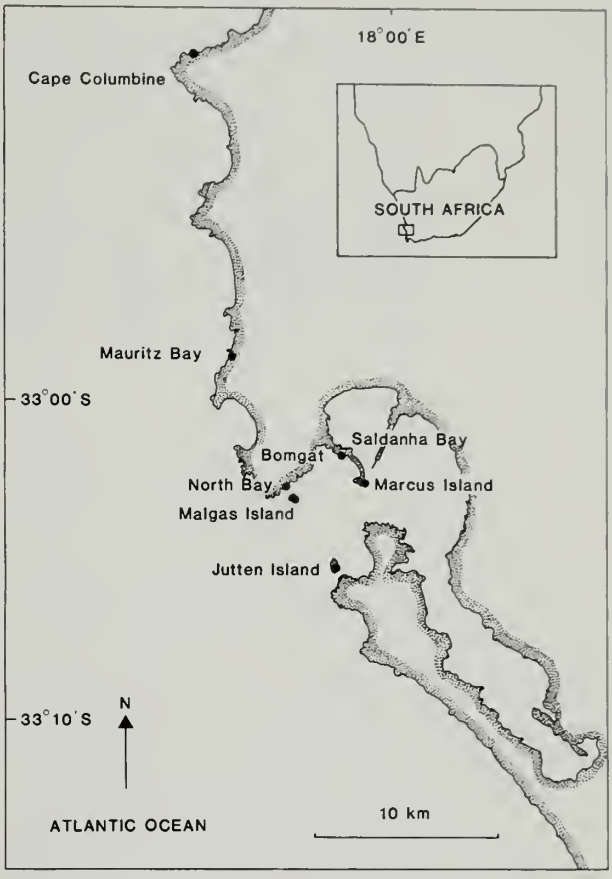

Figure 1

Map of the southwestern coast of South Africa, showing the Saldanha Bay area and the seven intertidal study sites.

METHODS AND MATERIALS

Study Sites

Seven intertidal study sites in the Saldanha Bay area (Figure 1) were visited monthly between December 1982 and April 1984. Three sites were on the shores of rocky, seabird-breeding islands (Malgas, Jutten, and Marcus islands). These sites are washed by nutrient-rich water, a consequence of the run-off of quantities of dissolved seabird guano (Bosman *et al.*, 1986). The rate of intertidal algal production on Jutten and Marcus islands is enhanced in response to this nutrient enrichment (Bosman & Hockey, 1986).

Two study sites (Mauritz Bay and Cape Columbine) were on the mainland shores outside the Bay (Figure 1), where no permanent aggregations of seabirds occur. Intertidal waters at these sites have relatively low nutrient concentrations, and the production rates of intertidal algae are slow in comparison with island sites (Bosman *et al.*, 1986; Bosman & Hockey, 1986). Two additional study sites were on mainland shores within the Bay (North Bay and Bomgat) and, although neither had regular aggregations of seabirds, both were considered to be within the possible zone of influence of nutrient enrichment from the seabird-breeding islands. The North Bay site has nutrient-rich intertidal waters as a result of current movement that transports guano run-off from Malgas Island to North Bay (Bosman & Hockey, 1986).

At all sites the granitic shore was gently sloping and exposed to strong wave action. Intertidal macroalgae comprised two dominant species—*Enteromorpha* sp. and *Porphyra capensis* (Kutz., 1849)—and the dominant intertidal herbivore (in terms of numbers and biomass) was the limpet *Patella granularis* (see Stephenson & Stephenson, 1972, for detailed description of intertidal communities). At unenriched mainland sites, where intertidal algal growth is slow, grazing by limpets prevents the development of foliose algae. In contrast, the intertidal algae at nutrient-rich sites form extensive, permanent mats (Bosman & Hockey, 1986). This is attributable both to the more rapid rate of algal production on island shores, and to the higher densities on these shores of oystercatchers, which remove *Patella granularis* (Hockey, 1981) and thereby may reduce the extent of herbivory.

All the sites except Mauritz Bay and Cape Columbine fall within areas of restricted access to the general public. Entry is by permit only and is strictly controlled. Mauritz Bay and Cape Columbine are accessible to the public, but are in areas of low human density. Local people on the west coast of South Africa do not exploit intertidal shellfish on a subsistence or a commercial basis (HOCKEY, in press; HOCKEY & BUXTON, in press) and disturbance to the limpet populations at Mauritz Bay and Cape Columbine is likely to be minimal. Fishermen and crayfish-divers were observed at these sites regularly but in low numbers.

Survival Rates

Each study site was divided into a low-, mid-, and high-shore region of equal area. In each region 50 *Patella granularis* were individually marked using punched plastic labels and rapidly setting epoxy glue. In subsequent months surviving individuals were located. If a limpet was absent in one month, but was located in a subsequent month, it was considered to have been present all the time. If a missing limpet was not located again it was considered dead. Limpets suffered mortality from predation and other factors, and when the number of marked individuals in any shore region fell below 10, supplementary limpets were labelled. The number of marked limpets present each month was used to estimate the finite rate of mortality per month and per year, using equations given by CAUGHLEY (1978). To test the durability of labels, 50 empty *P. granularis* shells were glued to the rock adjacent to the Marcus Island study site and were labelled *in situ*. The loss of labels was monitored during the subsequent seven months.

Influence of Limpet Size and Accessibility on Survival

Each month the shell lengths of surviving limpets were measured, and subsequently the survival rates of individuals smaller than 50 mm in length were considered separately from those of larger individuals. In addition, from April 1983 onwards, the position of each surviving limpet was recorded, and the mortality rates of those accessible to avian predators were considered separately from those of inaccessible individuals. Accessibility was determined subjectively using a knowledge of the morphology and feeding techniques of African black oystercatchers (HOCKEY, 1981). Oystercatchers were considered able to reach limpets on vertical or steep rock-faces if the limpets were less than 17 cm below the top (based on the depth to which oystercatchers reach to obtain limpets in rockpools—Hockey, unpublished data), or less than 40 cm from the bottom (based on the mean height and bill length of oystercatchers) of the rock-face. Accessibility was, however, ultimately determined in the field, as the presence of nearby rocky ledges on which birds could stand often made limpets on vertical rock-faces accessible. In cases where the accessibility of a limpet could not be ascertained clearly, the limpet was excluded from the analysis.

The influences of size and accessibility on the probability of a limpet's surviving for one month were determined using a generalized linear model (MCCULLAGH & NELDER, 1984) with a binomial error distribution and logit link function. The data were fitted using GENSTAT 4 (ALVEY *et al.*, 1983). The number of individuals present at the start of the month was equated with the number of trials, while the number surviving the month represented the number of successes. The roles of the independent variables in explaining variation in the probability of survival were expressed as a linear sum of the effects of each variable. The form of the model is thus

$$P = \frac{e^a}{1 + e^a}$$

where P is the probability of surviving one month and $a = b_0 + \sum_{i=1}^{n} b_i x_i$, where b_i are regression coefficients calculated by the model, and x_i are the explanatory variables, in this case study site, shore region, limpet size, and limpet accessibility.

Influence of Limpet Crypticity

Each month, between April 1983 and March 1984, the amount of foliose algal growth on the back of each relocated limpet was assessed in terms of the percentage of shell that was obscured from view. Percentages were grouped into categories 0, 1, and 2, being respectively, 0%, 1–50%, and >50% covered with algae. Seasonal trends in the proportions of limpets in each category at each site were analysed (with low-, mid-, and high-shore limpets considered together).

The influence of algal cover on the survival of small (<50 mm in length), accessible limpets also was determined using a generalized linear model with a binomial error distribution (see above). In this case the explanation of variation in the dependent variable (probability of surviving one month) is attempted using variations in the independent variables study site, shore region, and percentage algal cover.

RESULTS

Limpet Survival Rates

The plastic labels used to mark limpets were very durable: no labels were lost from the sample of 50 empty shells glued to the rocky shore, although entire shells were occasionally washed away. In some instances live limpets still bore their individual labels two years after being marked. Limpet survival rates measured at the study sites range from 94% month^{-1} (47% year^{-1}) in the mid-shore regions at Mauritz Bay and Malgas Island, to 77% month^{-1} (4% year^{-1}) in the low-shore region at the Marcus Island site (Figure 2). Limpets at the Jutten and Marcus Island sites have the lowest probability of survival (in all three

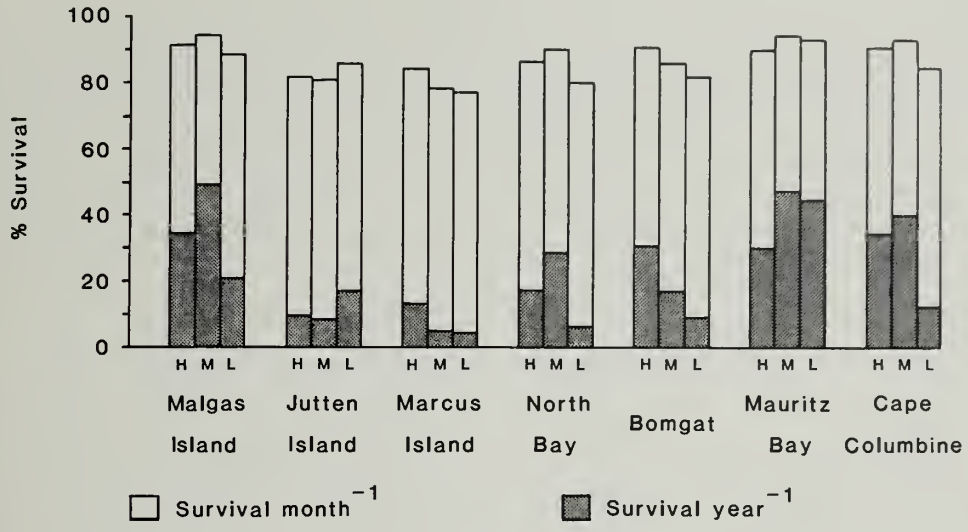

Figure 2

Survival rates of *Patella granularis* in the high- (H), mid- (M), and low-shore (L) regions at study sites in the Saldanha Bay area. Rates are calculated using mark-recapture techniques applied monthly over 12 months.

shore regions), while survival generally is highest at the mainland sites outside the Bay (Figure 2). Limpet survival rates recorded on the shores of Malgas Island are unexpectedly high, given the proximity of dense populations of oystercatchers.

Influence of Limpet Size and Accessibility

The generalized linear model best explaining variations in limpet survival rates ($X^2_{28} = 38.62$, $P > 0.10$) incorporated the independent variables study site, shore region, limpet size, and accessibility, as well as factors that accounted for interactions between site and region, and between site and limpet size (Table 1). The most significant correlate of limpet survival rate is limpet size (d.f. = 54, $t = 5.52$, $P < 0.005$—Table 1), indicating that limpets measuring 50 mm or more in length have an enhanced probability of survival. The survival of inaccessible and accessible limpets is not significantly different. The shore region in which a limpet occurs also influences its probability of survival. Limpets in the mid-shore region have significantly enhanced predicted survival rates (d.f. = 56, $t = 2.99$, $P < 0.002$) when compared with those in the low-shore region. In contrast, predicted limpet survival in the high-shore region is significantly reduced (d.f. = 56, $t = -1.91$, $P < 0.05$) when compared with survival in both other regions.

Although the relationships described above are applicable to all the study sites considered, the patterns may be modified by the unique influence of each study site. For example (see Table 1), the predicted probabilities of survival of limpets at the three island sites (Malgas Island coefficient is 0.00) are lower than at any other site, irrespective of the shore region involved or the sizes of the limpets concerned. Consequently, the predicted survival of limpets in different shore regions will be affected by differences between the sites. Similarly, although larger limpets are predicted to have a higher probability of survival, this relationship will be tempered by the unique influence of the site. This accounts for the importance of the interaction factors.

The benefit afforded a larger limpet, in terms of enhanced survival, decreases (coefficient becomes more negative) from island to mainland sites (see "Interactions" in Table 1). This is demonstrated clearly when the influences of all variables are taken into account and the survival rates (as predicted by the model) of limpets at island and mainland sites are compared (Table 2). Large limpets at island sites have consistently higher predicted probabilities of survival than do small limpets, whereas at mainland sites large limpets have reduced probabilities of survival. No limpets measuring more than 50 mm in length were recorded at Cape Columbine.

Influence of Algal Cover

On the shores of islands in Saldanha Bay the proportion of small, accessible limpets that are more than 50% covered by foliose algae peaks in the summer months, particularly between November and January (Figure 3). During the winter months most limpets are free of algal cover, although generally a few individuals support foliose algae in all months of the year. In contrast, limpets on mainland shores outside the Bay seldom support any foliose algae on their shells.

The generalized linear model initially used to explain variations in the survival rates of small, accessible limpets included the independent variable percentage algal cover, which was divided into categories 0, 1, and 2, being 0%, 1–50%, and >50% covered respectively. This model pre-

Table 1

Estimated coefficients, standard errors (SE), and significance levels generated when a generalized linear model is fitted to limpet survival rate data obtained from accessible and inaccessible limpets of two size classes: large are >50 mm and small are <50 mm in length.

Independent variable	Coefficient	SE	t	P (two-tailed)
Constant	1.01	0.161	6.84	<0.0005
Site				
Jutten Island	0.627	0.217	2.89	<0.005
Marcus Island	−0.225	0.225	−1.00	
North Bay	0.928	0.264	3.77	<0.0005
Bomgat	0.667	0.227	2.94	<0.002
Mauritz Bay	1.243	0.270	4.60	<0.0005
Cape Columbine	1.449	0.305	4.75	<0.0005
Shore-Region				
Mid-shore	0.771	0.258	2.99	<0.002
High-shore	−0.402	0.211	−1.91	<0.05
Limpet Size and Accessibility				
Large limpets (>50 mm)	1.112	0.201	5.52	<0.0005
Inaccessible limpets	0.137	0.171	0.80	
Interactions				
Jutten mid-shore	−1.116	0.334	−3.34	<0.001
high-shore	−0.788	0.280	−2.81	<0.005
Marcus mid-shore	0.030	0.339	0.09	
high-shore	0.899	0.295	3.04	<0.002
North Bay mid-shore	−0.208	0.435	−0.48	
high-shore	0.109	0.321	0.34	
Bomgat mid-shore	−0.507	0.352	−1.44	
high-shore	1.266	0.344	3.68	<0.0005
Mauritz mid-shore	−0.563	0.397	−1.42	
high-shore	0.578	0.354	1.63	
Cape Columbine mid-shore	−2.188	0.451	−4.85	<0.0005
high-shore	0.011	0.398	0.03	
Jutten large limpets	−1.017	0.277	−3.68	<0.0005
Marcus large limpets	−1.027	0.297	−3.46	<0.0001
North Bay large limpets	−1.928	0.414	−4.65	<0.0005
Bomgat large limpets	−1.942	0.351	−5.51	<0.0005
Mauritz large limpets	−1.753	0.386	−4.54	<0.0005

dicted no significant difference in the probability of survival of category 0 and 1 limpets (coefficient = −0.002, d.f. = 56, t = −0.02) and consequently the data for these two categories were combined. The generalized linear model best fitting the data (X^2_{36} = 41.04, $P > 0.20$) incorporated the independent variables study site, shore level, and percentage algal cover (0–50% or >50%) as well as a factor representing the interaction between site and shore region (Table 3).

Limpets that are more than 50% covered by foliose algae have a significantly enhanced monthly survival rate in comparison with limpets supporting less or no foliose algae (d.f. = 56, t = 1.67, P = 0.05). In addition, survival rate is highest in the mid-shore region (d.f. = 56, t = 2.47, $P < 0.01$) and lowest in the high-shore region (d.f. = 56, t = −1.77, $P < 0.05$), as was found in the previous model.

Differences in attributes of study sites explained the largest amount of variation in survival rates (Table 3), with the predicted probability of survival being lowest at Malgas (coefficient = 0.00) and Marcus islands, and highest at Mauritz Bay. Limpets at Cape Columbine have an unexpectedly low probability of survival, but when all independent variables are taken into account the interaction between site and shore region compensates for this (Figure 4). Limpet survival rate, as predicted by this model for each shore region at each site, is enhanced in the case of limpets that are more than 50% covered by foliose algae (Figure 4). The predicted benefit to algal-covered limpets, in terms of enhanced survival, is greater at island sites than at mainland sites (Figure 4), with the benefit being least (an increase of 1% in predicted monthly survival rate) in the high- and mid-shore regions at Cape Columbine.

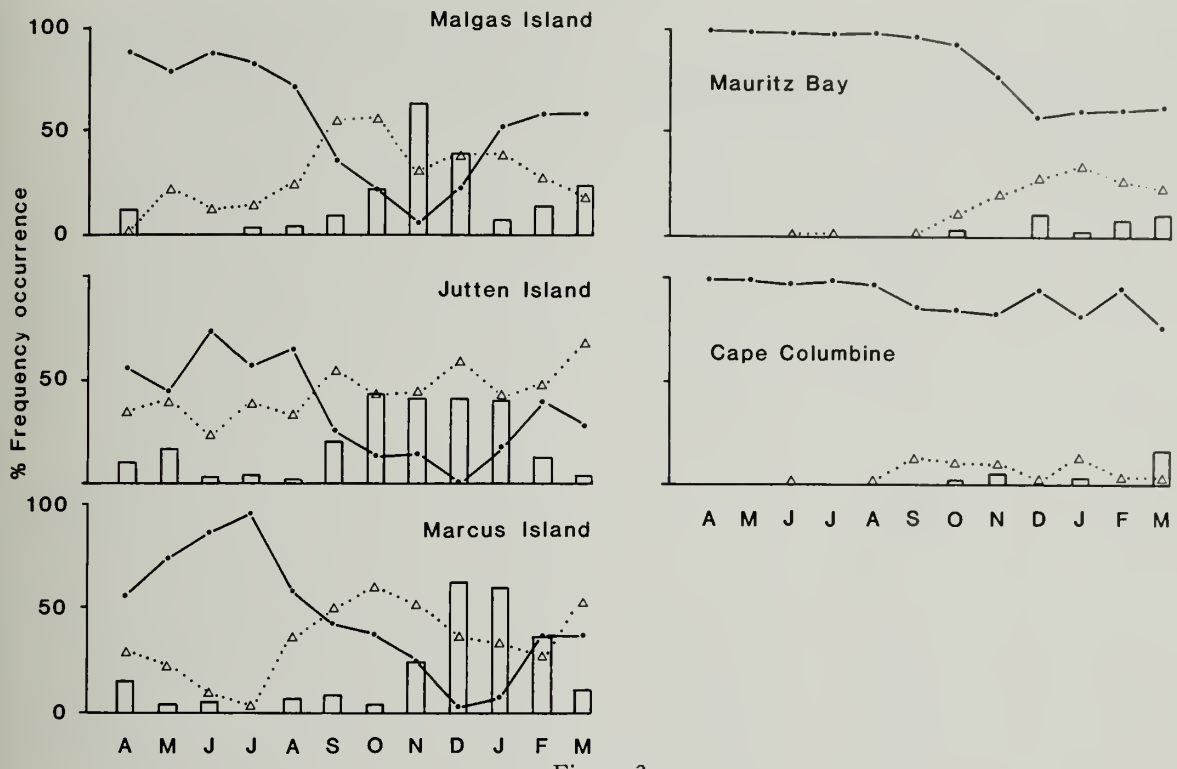

Figure 3

Seasonal changes in the proportions of *Patella granularis*, on island and mainland shores, that support 0% (solid line), 1–50% (dotted line), and >50% (histograms) algal cover on their shells.

DISCUSSION

Limpet Survival Rates

Patella granularis is the most abundant species of limpet in the mid- and high-shore regions of rocky shores on the west coast of southern Africa. It is prominent in the diet of African black oystercatchers, comprising between 24 and 90% of all prey items fed to chicks on the islands off the west coast (HOCKEY & UNDERHILL, 1984). In addition, oystercatchers affect the density and population size structure of limpets accessible to predation on the shores of these islands (HOCKEY & BRANCH, 1984), indicating the major impact of predation by these birds. Other potential predators of *P. granularis* include kelp gulls, *Larus dominicanus* (Licht., 1823), and the giant clingfish, *Chorisochismus dentex* (Pallas, 1769), but limpets are eaten only occasionally by these species (STOBBS, 1980; ARMSTRONG, 1984). The density of African black oystercatchers on islands in Saldanha Bay ranges from 25 (winter count on Malgas Island) to 78 birds per km coast (summer count on Jutten Island—HOCKEY, 1983). In comparison, the mainland coast in the area of the North Bay and Bomgat sites supports between 2 and 16 birds per km coast, and mean density of oystercatchers recorded on mainland shores outside the Bay is 3.6 birds per km coast (HOCKEY, 1983).

Limpet mortality rates measured in the Saldanha Bay area (Figure 2) are highest on the shores of Jutten and Marcus islands, although these rates are not as high as the mortality rate of *Patella vulgata* (L., 1758) (90% month^{-1}) in the presence of European oystercatchers, *Haematopus ostralegus* (L., 1758), reported by LEWIS & BOWMAN (1975). In their study however, oystercatchers were present in large flocks on rocky shores in Yorkshire on a seasonal and transient basis, whereas African black oystercatchers are resident on the shores of islands in Saldanha Bay. Recorded limpet mortality rates were lowest on the mainland shores at Mauritz Bay and Cape Columbine, and intermediate at the North Bay and Bomgat sites (Figure 2). Variations in the survival rates of *P. granularis* at different study sites may be attributed largely to variations in the density of oystercatchers, and consequently, in predatory pressure.

Within each study site, predicted limpet survival is lowest in the high-shore region, possibly reflecting the more stressful physical conditions prevalent in that region (JERNAKOFF, 1983). Limpets in the low-shore region do not have to contend with high temperatures or desiccation as frequently, since they are submerged for a large proportion of the tidal cycle. However, oystercatchers show a peak in foraging activity at the time of low tide (HOCKEY,

Table 2

Monthly limpet survival rates predicted by the generalized linear model fitted to survival rate data from accessible and inaccessible limpets in two size categories (small are <50 mm, large are >50 mm) in three regions of the shore (H = high-shore, M = mid-shore, L = low-shore).

Site	Shore region	Accessible		Inaccessible	
		Small	Large	Small	Large
Malgas Island	H	0.67	0.86	0.70	0.88
	M	0.87	0.95	0.88	0.96
	L	0.75	0.90	0.78	0.91
Jutten Island	H	0.63	0.65	0.66	0.68
	M	0.80	0.81	0.82	0.83
	L	0.85	0.86	0.87	0.88
Marcus Island	H	0.80	0.81	0.82	0.83
	M	0.84	0.85	0.86	0.87
	L	0.71	0.72	0.73	0.75
North Bay	H	0.85	0.72	0.87	0.74
	M	0.93	0.86	0.94	0.87
	L	0.88	0.77	0.90	0.79
Bomgat	H	0.93	0.86	0.94	0.87
	M	0.88	0.77	0.90	0.79
	L	0.85	0.72	0.87	0.75
Mauritz Bay	H	0.93	0.87	0.93	0.88
	M	0.93	0.87	0.94	0.89
	L	0.91	0.85	0.92	0.86
Cape Columbine	H	0.90	*	0.91	*
	M	0.76	*	0.78	*
	L	0.93	*	0.94	*

* No limpets of greater than 50 mm in length were recorded at Cape Columbine.

1984) and tend to forage at the water's edge (Hockey, 1981), rendering low-shore limpets more likely to be removed than mid-shore limpets.

Influence of Limpet Size

The most significant correlate of limpet survival rate is limpet size. African black oystercatchers select limpets of between 20 and 40 mm in length, and are unlikely to be successful in removing individuals of more than 60 mm in length (Hockey & Underhill, 1984). Consequently, larger limpets have a refuge in size. This is particularly important on the shores of seabird-breeding islands in Saldanha Bay where limpet growth rate is rapid (Bosman & Hockey, in press) and individuals soon reach a size at which they are free from oystercatcher predation. At these sites larger limpets are predicted to have enhanced survival rates (Table 2). In particular, limpets on the Malgas Island shores are affected by this relationship as the population at this site is dominated by very small and very large individuals (5.8% are greater than 60 mm in length, whereas at Cape Columbine limpets of greater than 50 mm in length do not occur—Hockey & Branch, 1984; Bosman & Hockey, in press). Small individuals (<15 mm in length) are not suitable for labelling and consequently, although limpets larger than 50 mm were labelled in proportion to their occurrence in the population at the Jutten and Marcus Island sites (14% and 13% respectively), the larger limpets constitute 33% of the individuals labelled on the shore of Malgas Island. The survival rate recorded on Malgas Island for the limpet population as a whole is thus artificially high.

In contrast, limpets on mainland shores do not benefit

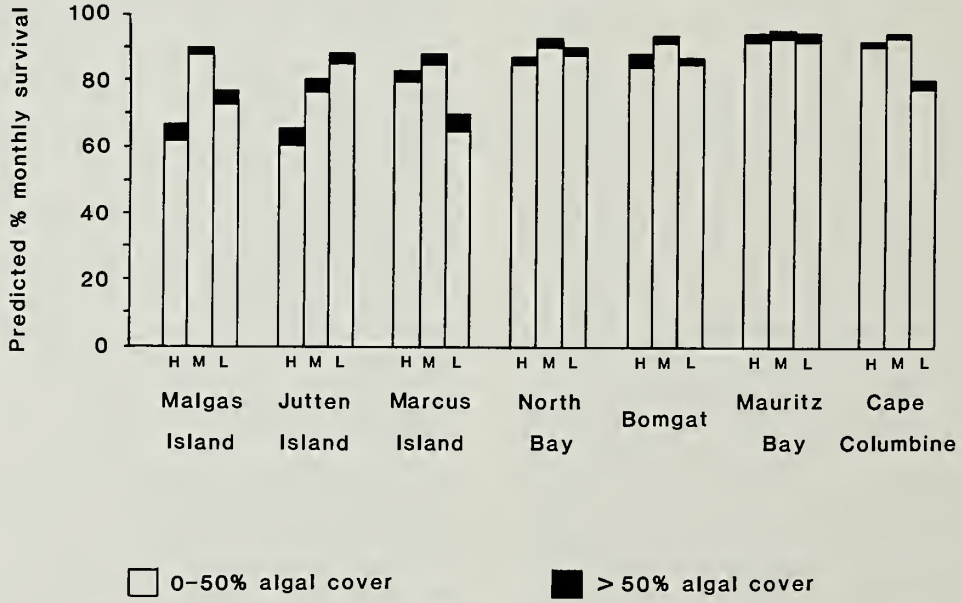

Figure 4

Predicted survival rates of small (<50 mm), accessible *Patella granularis* in the high- (H), mid- (M), and low-shore (L) regions at intertidal study sites. Shaded areas represent the predicted enhancement in survival afforded by a >50% covering of foliose algae.

Table 3

Estimated coefficients, standard errors (SE), and significance levels generated when a generalized linear model is fitted to limpet survival rate data obtained from small (<50 mm), accessible limpets with variable amounts of foliose algae on their shells.

Independent variable	Coefficient	SE	t	P (two-tailed)
Constant	0.990	0.173	5.72	<0.0005
Site				
Jutten Island	0.804	0.232	3.47	<0.0005
Marcus Island	−0.365	0.238	−1.53	
North Bay	0.975	0.251	3.88	<0.0005
Bomgat	0.717	0.236	3.03	<0.002
Mauritz Bay	1.446	0.290	4.99	<0.0005
Cape Columbine	0.245	0.325	0.78	
Shore-Region				
Mid-shore	0.978	0.395	2.47	<0.01
High-shore	−0.495	0.280	−1.77	<0.05
Algal Cover				
>50% cover	0.231	0.138	1.67	=0.05
Interactions				
Jutten mid-shore	−1.564	0.466	−3.35	<0.001
high-shore	−0.858	0.344	−2.49	<0.01
Marcus mid-shore	0.114	0.464	0.25	
high-shore	1.258	0.365	3.45	<0.001
North Bay mid-shore	−0.587	0.517	−1.13	
high-shore	0.273	0.374	0.73	
Bomgat mid-shore	−0.632	0.468	−1.35	
high-shore	0.511	0.548	0.93	
Mauritz Bay mid-shore	−0.793	0.514	−1.54	
high-shore	0.524	0.417	1.26	
Cape Columbine mid-shore	0.318	0.547	0.58	
high-shore	1.510	0.461	3.28	<0.001

by being large, and the predicted probabilities of survival are lower for large individuals than for small ones at the same site (Table 2). Limpets have slower growth rates on mainland shores than on islands (Bosman & Hockey, in press) and, since maximum adult size attainable by an individual is a function of its growth rate (Branch, 1974b; Balaparameswara Rao, 1976), limpets on unenriched mainland shores never attain sizes comparable with those on islands. Large limpets on an unenriched mainland shore are thus older than similarly-sized individuals on an island shore, and may experience higher mortality due to senescence.

Influence of Accessibility and Crypticity

Limpets inaccessible to oystercatchers automatically achieve a refuge from predation by birds, irrespective of their growth rate and size. *Patella granularis* exhibits homing behavior and will return to a home scar during periods of inactivity and environmental stress, *e.g.*, during the daytime low-tide period (Branch, 1971). In this study 89% of limpets that were recorded as being inaccessible in a month, and that survived at least three subsequent months, were recorded as inaccessible on all four visits; yet the model used predicted no advantage (in terms of limpet survival) to this behavior (Table 1). *Patella granularis* forages at night (Branch, 1971) and those individuals recorded as inaccessible during day-time visits to a study site may have become accessible during the night (particularly those on the walls of crevices in the rock). Oystercatchers also forage at night, and Hockey & Underhill (1984) showed that on Jutten Island limpets formed a higher proportion of oystercatcher prey items at night than during the day. Given such conditions, few limpets in this study probably were truly inaccessible to oystercatchers.

Oystercatchers forage using visual cues and have been shown to discriminate between the anterior and posterior shell margins when attacking limpets (Hockey, 1981; Hockey & Branch, 1983). Foliose algae that develop on the shell of a limpet and that obscure 50% or more of the individual render it less likely to be recognized as a prey item and significantly enhance its probability of survival. The probabilities of survival of limpets without algae and those with 1–50% cover are not different, indicating that it is the escape from predation afforded by the algal cover, rather than the amelioration of temperature and desiccation stresses, that leads to enhanced survival.

The development of algae on the shells of marine and

intertidal organisms has been documented in several instances (SINCLAIR, 1963; BOUXIN, 1964; BRANCH, 1971) but no advantages have been demonstrated to accrue to affected individuals. In the Saldanha Bay area foliose algae develop on *Patella granularis* shells during the months when rates of algal production are fastest (BOSMAN & HOCKEY, 1986), and the development of algal covering is most profuse and widespread on island shores (Figure 3). The effect of an algal covering on limpet survival rate is apparent (albeit very slight) on mainland shores, but is more pronounced on the shores of islands, where oystercatcher predatory pressure is intense (Figure 4), once again indicating that the primary advantage of an algal covering is the camouflage it provides.

Differential Survival Rates: Their Impact on Prey Population Dynamics

The selective removal of certain prey size classes by avian predators may have a significant impact on the demography and dynamics of the prey population. HOWARD & LOWE (1984) found that selection by royal spoonbills, *Platalea regia* (Gould, 1838), of the largest and slowest-moving caridean shrimps in seagrass beds leads to a disproportionately high mortality of adult females. Females attain larger body sizes than males, and may be hampered, when attempting to escape, by the mass of the large clutch of eggs. There is a resultant skewed sex ratio in the population, and female longevity and life-time reproductive output are reduced. On the rocky shores of islands in Saldana Bay predation by oystercatchers results in high mortality of medium-sized limpets. However, the rapid growth rates of limpets on island shores, and the inability of oystercatchers to handle large limpets, ensure that a certain proportion of individuals attain a refuge from predation by virtue of their size.

Limpet gamete production increases exponentially with respect to an increase in shell length (BRANCH, 1974a), and HOCKEY & BRANCH (1984) estimate that as much as 86% of the female gametic material released by limpets on the shores of Jutten Island is derived from limpets that have a refuge in size. The reproductive effort of these individuals probably is vital to the system's continued ability to support dense populations of oystercatchers. Oystercatchers are uncommon on mainland shores (particularly outside the Bay) where the rate of limpet growth is slow and even the largest and most fecund limpets would be available to the birds.

The demography and reproductive output of limpet populations on the shores of seabird-breeding islands are modified by the effects of oystercatcher predation. The size structure of prey populations is altered (HOCKEY & BRANCH, 1984), and the average survival rates and lifetime reproductive outputs of individuals are reduced. The reproductive output of the prey population may be maintained by virtue of a refuge in size for large individuals and, to a lesser extent, by the crypticity resulting from the development of foliose algae on the shell of the prey.

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Correlation of Live Mollusks with Sediment and Bathymetry on the Texas Inner Shelf[1]

by

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Abstract. An extensive survey of the macroinvertebrate populations of the Gulf of Mexico on the inner shelf of the Texas coast was initiated in 1976. The focus of this inventory was (1) identification and enumeration of the macrofauna, (2) description of faunal communities, and (3) correlation of distribution and abundances, including sediment and faunal relationships. This report summarizes the molluscan data from that survey. Although other inventories of mollusks on the inner shelf have been undertaken, this is the most extensive regional survey conducted on the Texas Gulf Coast.

One hundred forty-one species of mollusks (82 gastropods, 56 bivalves, and 3 scaphopods) were found in 554 benthic samples from stations located 1–11 miles (1.6–17.6 km) offshore from Sabine Pass to Brownsville, Texas. Both numbers of species and numbers of individuals of gastropods, bivalves, and scaphopods are greater on the South Texas inner shelf (Brownsville to Corpus Christi) than in areas northeast of Corpus Christi.

Cluster analysis separated the fauna into three assemblages—a nearshore assemblage, characterized by sandy substrates, a transitional assemblage characterized by substrates of sandy mud, and an outer assemblage characterized by substrates of less-sandy mud. All three are found on the inner shelf except in the Port Lavaca and Beaumont-Port Arthur areas. Faunal-sediment associations indicate that more molluscan species occur in sand than in mud, and the most abundant species are found where the sand fraction is high (80–100% sand). Analysis of the bathymetric distribution of mollusks shows that the mean number of species is highest in a depth range of 18–60 ft (6–18 m). Many species are most abundant at either shallower-water stations (stations from 18.0–36.1 ft or 5.5–11.0 m deep) or deeper-water stations (stations from 47.9–60.0 ft or 14.6–18.3 m deep).

INTRODUCTION

Molluscan populations from the inner shelf of the Texas coast were studied in 6672 surficial bottom samples, including 3940 from the inner shelf and 2732 from the bay-estuary-lagoon system, collected at regularly spaced intervals of 1 mi (1.6 km). This inventory of the State-owned submerged lands (Figure 1) provides an extensive spatial data base on sediment texture, sediment geochemistry, and benthic macroinvertebrates. The focus of the biological analyses was (1) identification and enumeration of the macrofaunal species, (2) identification and delineation of characteristic faunal assemblages, (3) correlation of dis-

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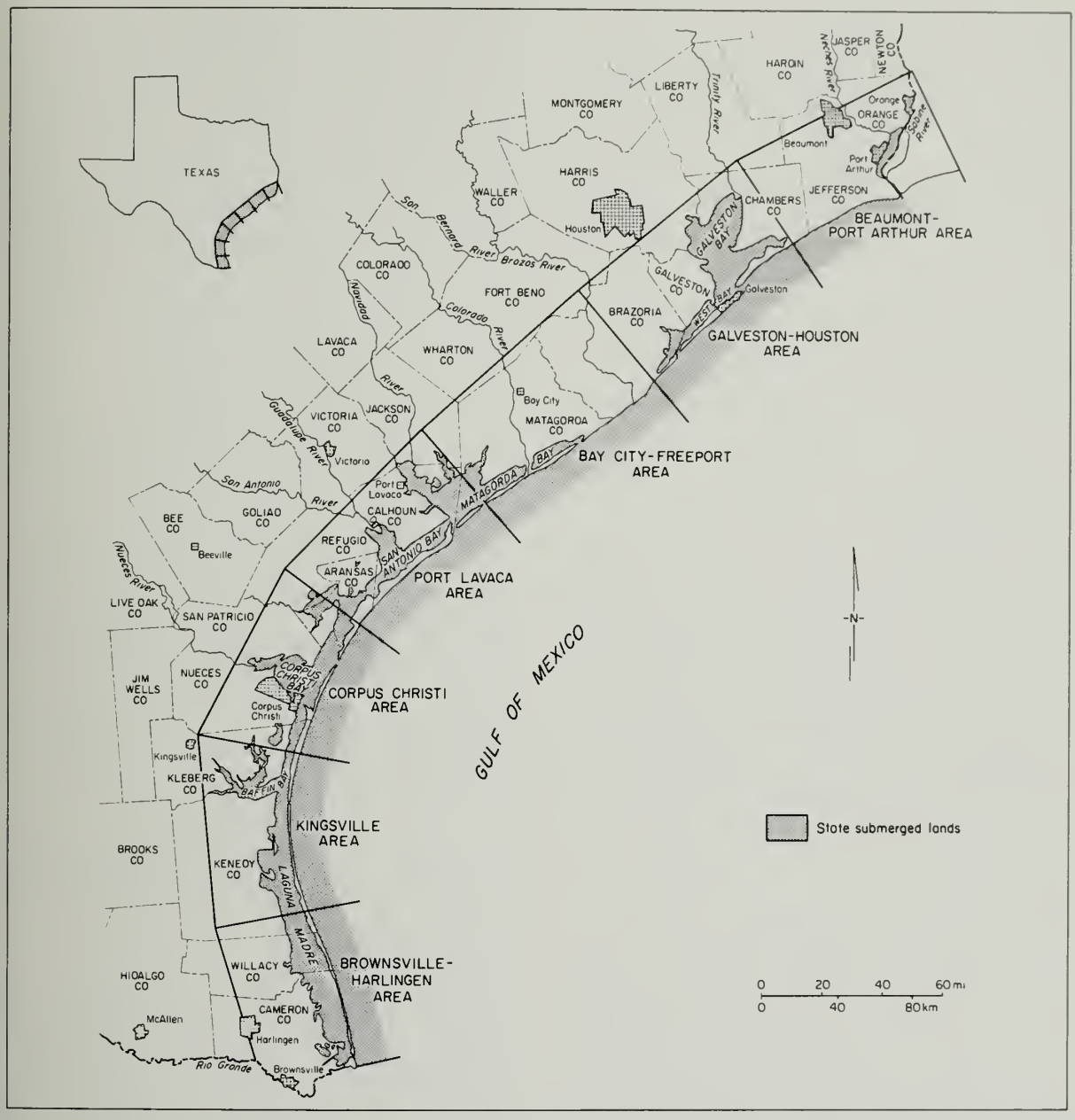


Figure 1

Index map showing seven areas that include the submerged coastal lands of Texas (modified from McGowen & Morton [1979] and Brown [1972–1980]).

tributions and abundances with physical and biotic factors, and (4) faunal relationships. Records are for live-collected animals except as noted.

Maps and reports derived from the study are being published as a series of atlases of the Texas coast, divided into seven areas (Figure 1) similar to those defined in Brown (1972–1980) and in McGowen & Morton (1979). Atlases available for Corpus Christi (White *et al.*, 1983), Galveston-Houston (White *et al.*, 1985), Brownsville-Harlingen (White *et al.*, 1986), Beaumont-Port Arthur (White *et al.*, 1987), and Bay City-Freeport (White *et al.*, 1988) areas contain discussions on the distribution of mollusks, polychaetes, and crustaceans. Each atlas has sections on invertebrate distributions related to sediment and bathymetry, benthic assemblages, and species diversity, and an appendix listing species, numbers of individuals, and locality data. Dead-collected mollusks were also identified and listed, but because of time and financial

Table 1

Number of stations examined and sampling dates.

Area	Number of stations	Dates
Brownsville-Harlingen	113	April 1976
Kingsville	81	March and April 1976
Corpus Christi	73	May 1976
Port Lavaca	72	May and October 1976
Bay City-Freeport	79	October 1976
Galveston-Houston	80	October 1976; September 1977
Beaumont-Port Arthur	56	October 1976; September 1977

constraints, individual counts of these were made only in the Corpus Christi (WHITE *et al.*, 1983) and Galveston-Houston (unpublished data) areas.

Many other studies have discussed the shallow-water mollusks from the Texas coast. ANDREWS (1977) and MOORE (1979) summarized early studies concerned primarily with mollusks, and TREECE (1979) listed mollusks from the South Texas continental shelf. PARKER (1960), DEFENBAUGH (1976), FLINT & RABALAIS (1981), and HILL *et al.* (1982) included mollusks in their assemblage studies of the Texas inner shelf. Substrate-faunal relationships were investigated by HILL *et al.* (1982) on the South Texas shelf, HARPER *et al.* (1981) on the Bay City-Freeport area, HARPER (1970) on the Galveston-Houston area, and HULINGS (1955) and KENNEDY (1959) on the Beaumont-Port Arthur area.

Most earlier studies have data from only a few stations on the inner shelf or are limited geographically to a specific area. This study, however, although it does not examine seasonal fluctuations in molluscan populations, is an extensive regional survey of the Texas Gulf Coast having greater sample density than do earlier studies and includes the entire inner shelf from Brownsville to Sabine Pass. Such an extensive study allows more accurate delineations of molluscan distributions and a better measure of their diversity. Additionally, identification, mapping, and characterization of inner-shelf molluscan populations provide an important spatial data base that is useful in predicting and measuring the effects of a multitude of activities (such as food production, energy production, recreation, resource extraction, industrial processing, and transportation) on the coastal ecosystem.

MATERIALS AND METHODS

Surficial sediment samples analyzed for this study were taken with a Smith-McIntyre grab sampler (capacity of 0.46 ft^3 or 0.013 m^3) at sites spaced approximately 1 mile (1.6 km) apart on the inner continental shelf to a distance of about 11 miles (17.6 km) seaward of the Gulf shoreline. One grab was taken at each station. Of the 3940 inner-shelf samples collected, 554 (14%) were analyzed for mollusks. The numbers and locations of samples analyzed were determined in part by the necessity for establishing an adequate data base for mapping and interpretation and, at the same time, by the need to consider time requirements and costs. Sample-collection dates and numbers of samples examined from each area are given in Table 1. Bathymetric data were derived from National Ocean Survey maps. Smooth sheets with original soundings and survey lines taken in 1938 and 1939 were used for inner-shelf bathymetry between the Rio Grande and Pass Cavallo; navigation charts derived from similar surveys provided bathymetry along the remainder of the central and upper coast (MCGOWEN & MORTON, 1979).

Shelf sediments were washed through either a 0.5- or a 1-mm sieve, narcotized with propylene phenoxytol, and stored in a neutral solution of 10% formalin containing rose bengal. Laboratory processing included further washing and storing in 70% ethanol.

Live-collected mollusks were separated from dead ones, then identified and counted. Although dead individuals of species were not counted, species that were collected dead were listed for each station.

Analyses of the sediment included quantitative determination of the gravel, sand, and mud fractions in each sample, followed by more detailed textural analyses of the sand and mud fractions. Sediment types are classified on the basis of relative percentages, in accordance with the triangular classification system shown in MCGOWEN & MORTON (1979), in which shell (gravel), sand, and mud are the end members of the triangle. Size distribution in the coarse fraction (>0.0625 mm) was determined by a rapid sediment analyzer (SCHLEE, 1966); size distribution in the mud (silt [0.0625 to 0.0039 mm] and clay [<0.0039 mm]) fraction was determined by Coulter Counter techniques (SHIDELER, 1976).

Cluster analysis was used to delineate benthic communities. All macrobenthic species (primarily polychaetes, crustaceans, and mollusks) were included in the analyses; however, data reduction was often necessary because of the limited capacity of the cluster program. The Canberra metric dissimilarity coefficient was used along with flexible sorting on the dissimilarity coefficients (CLIFFORD & STEPHENSON, 1975). For more details concerning computer procedures, see WHITE *et al.* (1987).

RESULTS AND DISCUSSION

One hundred forty-one species of mollusks were collected from the inner shelf, consisting of 82 gastropods, 56 bivalves, and 3 scaphopods. Numbers of molluscan species and individuals generally decrease from south to north (Figures 2, 3). Therefore, numbers of species and individuals of all three classes (Gastropoda, Bivalvia, and Scaphopoda) are more abundant on the South Texas inner shelf from Brownsville to the Corpus Christi area than they are

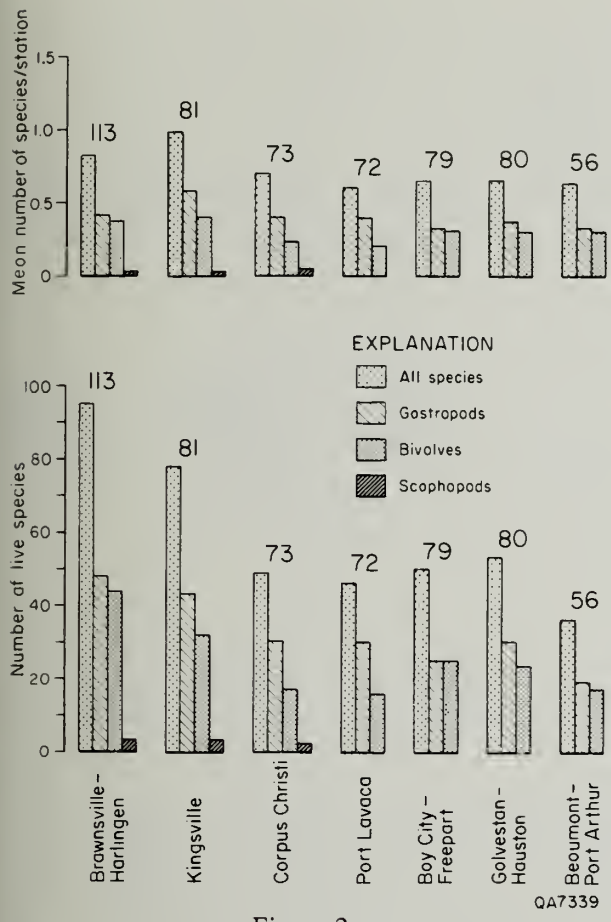


Figure 2

Numbers of molluscan species in the seven study areas. Numbers above bars equal number of stations examined in each area.

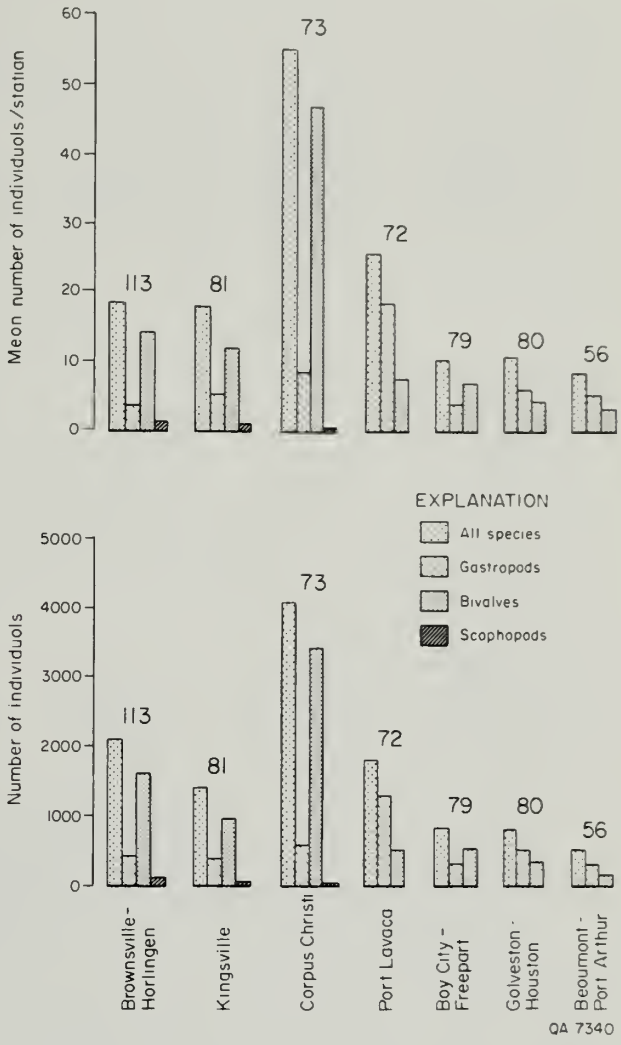


Figure 3

Numbers of mollusk individuals in the seven study areas. Numbers above bars equal number of stations examined in each area.

between Corpus Christi and the Beaumont-Port Arthur area. The mean number of bivalve species per station (Figure 2) is highest in the Brownsville and Kingsville areas, whereas the mean number of bivalve individuals per station (Figure 3) is highest in the Corpus Christi area, primarily because of the large number of *Abra aequalis* (Say, 1822). Of the 3242 individuals of *Abra* recovered from the Corpus Christi area, more than 50% were recovered from one station. If individuals of *Abra* were not included in counts of individual bivalves from each of the seven areas, then the number of bivalve individuals would be three times higher in the Brownsville-Harlingen area than in any of the other six areas.

Gastropod species are generally more abundant than bivalve or scaphopod species. Gastropod species are most numerous in the Brownsville and Kingsville areas (Figure 2), whereas both the mean number of individuals per station and the total number of individuals per station are highest in the Port Lavaca area (Figure 3), primarily because of the large numbers of *Nassarius acutus* (Say, 1822) recovered from the Port Lavaca area. Scaphopods (three species) were recovered only in the Brownsville-Harlingen, Kingsville, and Corpus Christi areas.

Several bivalve and gastropod species are most abundant (according to percent of the total number of stations) either on the southern (Brownsville-Harlingen, Kingsville, or Corpus Christi) or northern (Beaumont-Port Arthur or Galveston-Houston) coast (Figure 4). Species most abundant overall on the southern coast include *Linga amiantus* (Dall, 1901), *Parvilucina multilineata* (Toumey & Holmes, 1857), *Nucula proxima* Say, 1822, *Anadara transversa* (Say, 1822), and *Diplodonta soror* C. B. Adams, 1852. Abundant northern-coast species include *Nuculana concentrica* (Say, 1824), *Nassarius acutus* (Say, 1822), and *Parvanachis obesa* (C. B. Adams, 1845). *Abra aequalis* (Say, 1822) and *Natica pusilla* (Say, 1822) are abundant in all seven areas (Figure 4).

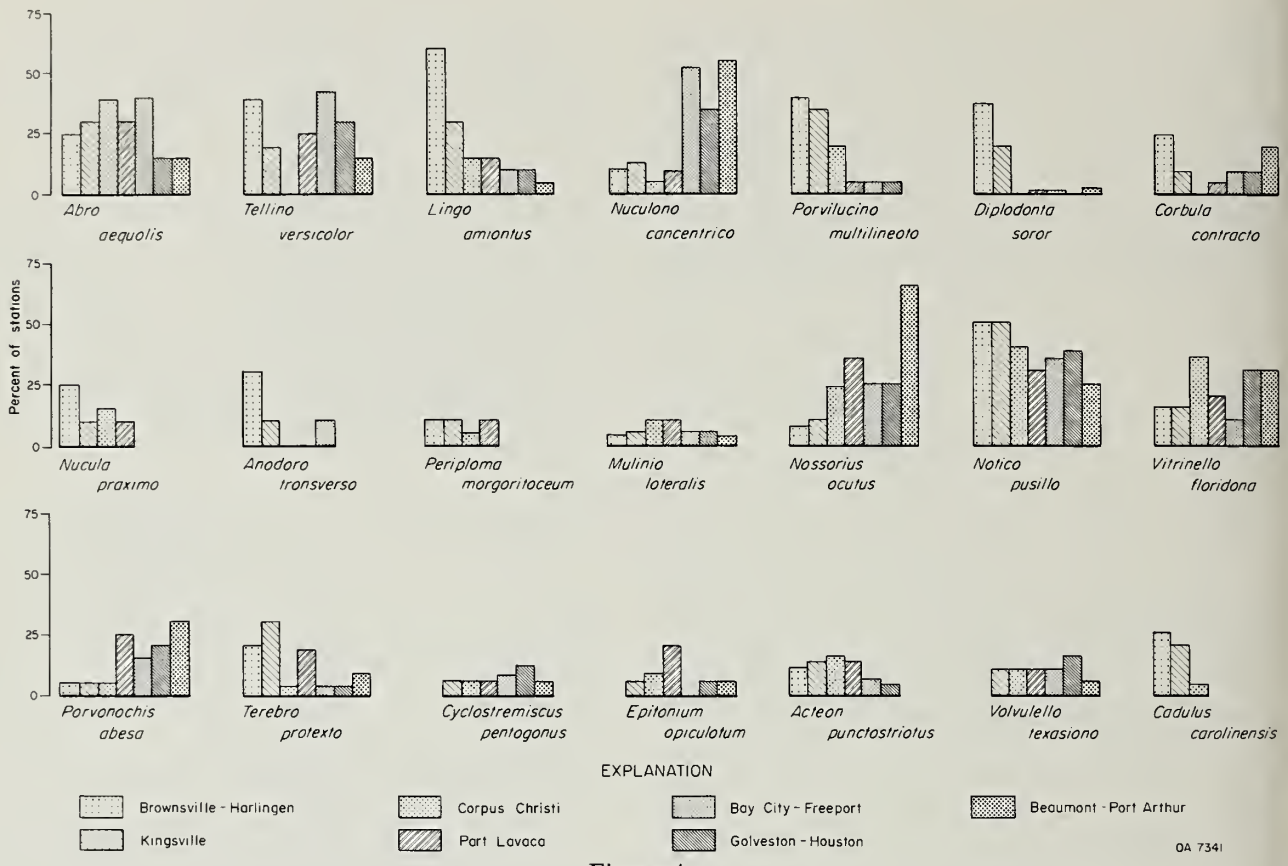


Figure 4

Distribution of some of the abundant mollusks according to the percentage of all stations in the seven study areas.

Assemblages

Cluster analysis separated the inner-shelf fauna (primarily polychaetes, mollusks, and crustaceans) into three assemblages—a nearshore assemblage characterized by sandy substrates (average of 81% sand), a transitional assemblage characterized by substrates of sandy mud (average of 43% sand), and an outer assemblage with substrates of less-sandy mud (average of 28% sand). All three assemblages are present on the inner shelf except in the Beaumont-Port Arthur area, which lacks the nearshore assemblage, and the Port Lavaca area, which has no outer assemblage (Figures 5, 6). The mean numbers of species and individuals per station are highest in the nearshore assemblage and lowest in the outer assemblage (Table 2).

Most of the abundant mollusks can be separated into five species groups (Figure 7) according to their frequency of occurrence within the three assemblages. Frequency of occurrence is defined as the percentage of the total number of stations in which a species is found in an assemblage. Species group I contains five species (*Natica pusilla, Abra aequalis, Tellina versicolor* DeKay, 1843, *Nassarius acutus,* and *Linga amiantus*) that are abundant in all assemblages; species in groups II (*Parvilucina multilineata, Acteon punctostriatus* (C. B. Adams, 1840), *Mulinia lateralis* (Say, 1822), *Periploma margaritaceum* (Lamarck, 1801), *Parvanachis obesa, Epitonium apiculatum* (Dall, 1889), and *Oliva sayana* Ravenel, 1834) and III (*Diplodonta soror, Terebra protexta* Conrad, 1845, *Cadulus carolinensis* Bush, 1885, and *Anadara transversa*) are most abundant in the nearshore or transitional assemblage, respectively; species in group IV (*Vitrinella floridana* Pilsbry & McGinty, 1946, *Nuculana concentrica, Nucula proxima, Corbula contracta* Say, 1822, and *Volvulella texasiana* Harry, 1967) are most abundant in the transitional or outer assemblage; and species in group V (*Turbonilla* sp. B, *Cantharus cancellarius* (Conrad, 1846), *Cyclostremiscus pentagonus* (Gabb, 1873), *Dentalium texasianum* Philippi, 1848, and *Nuculana acuta* (Conrad, 1831)) are not abundant in any assemblage.

Parker (1960) described an inner-shelf assemblage between depths of 10 and 66 ft (3–20 m) located primarily along the central coast in the Port Lavaca and Corpus Christi areas. Characteristic mollusks included the bivalves *Atrina serrata* (Sowerby, 1825), *Dinocardium robustum* (Lightfoot, 1786), *Dosinia discus* (Reeve, 1850), *Raeta plicatella* (Lamarck, 1818), and *Spisula solidissima* (Dillwyn, 1817). Stanton & Evans (1971) delineated two

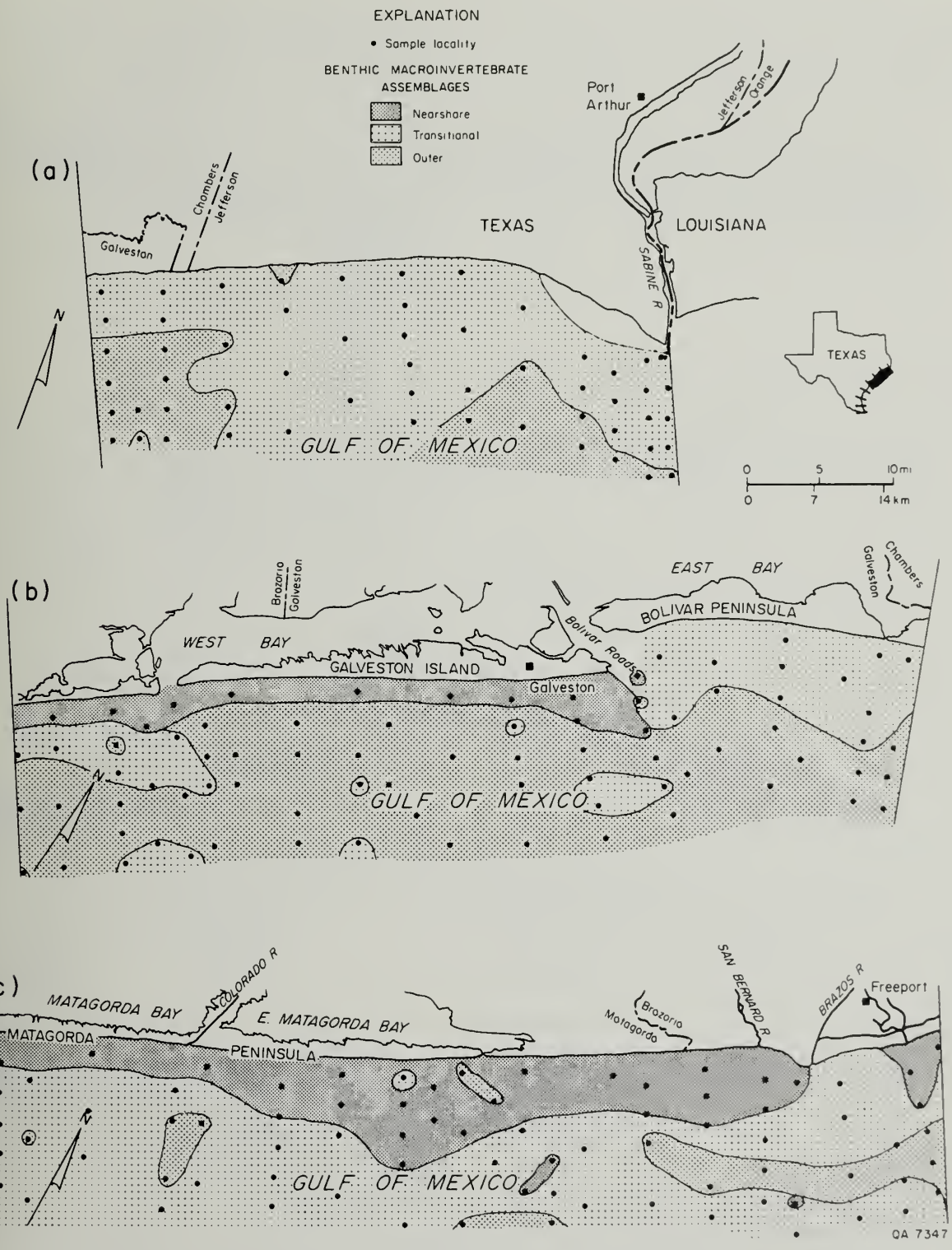


Figure 5

Benthic macroinvertebrate assemblages and sample localities in the Beaumont-Port Arthur (a), Galveston-Houston (b), and Bay City-Freeport (c) areas.

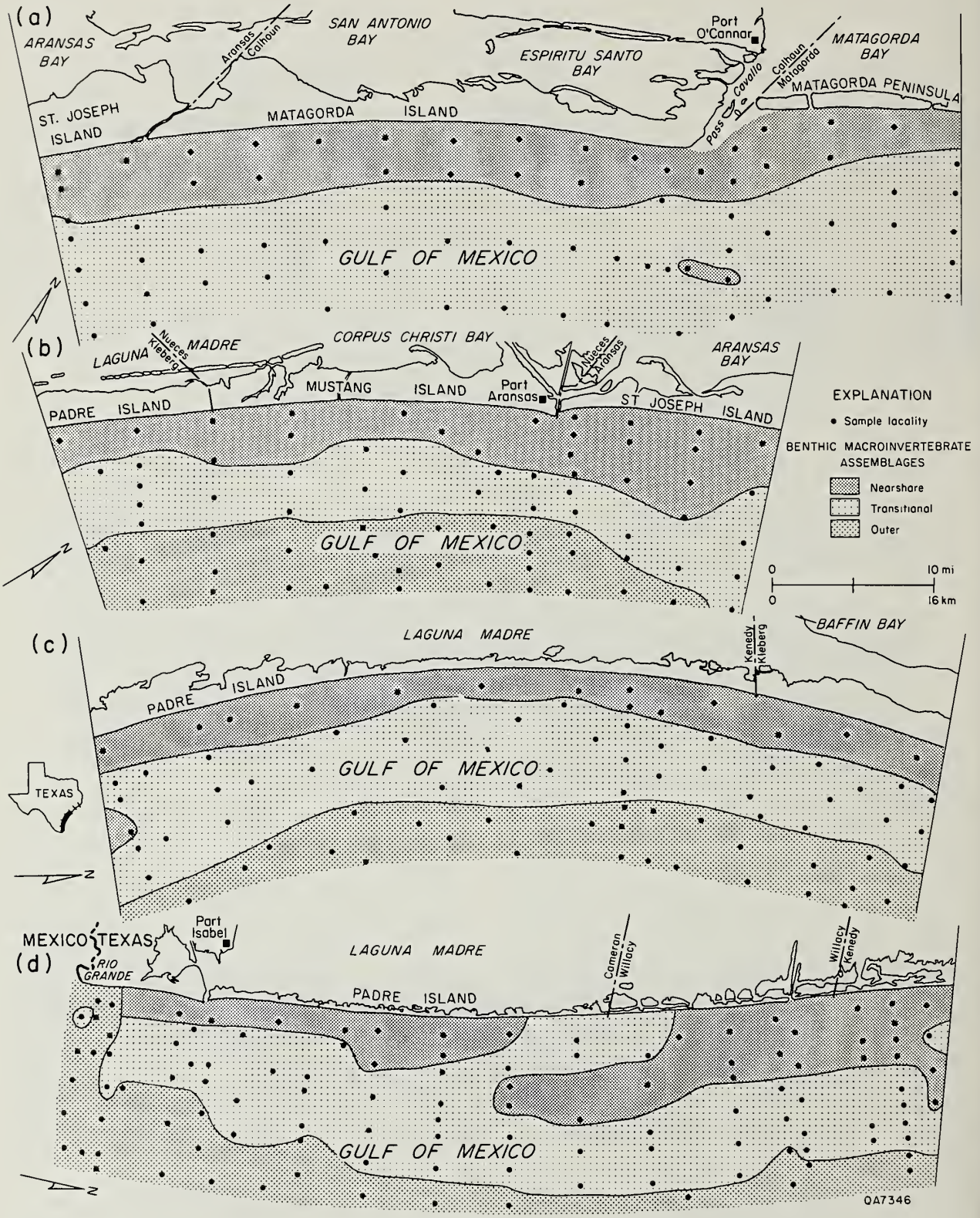


Figure 6

Benthic macroinvertebrate assemblages and sample localities in the Port Lavaca (a), Corpus Christi (b), Kingsville (c), and Brownsville-Harlingen (d) areas.

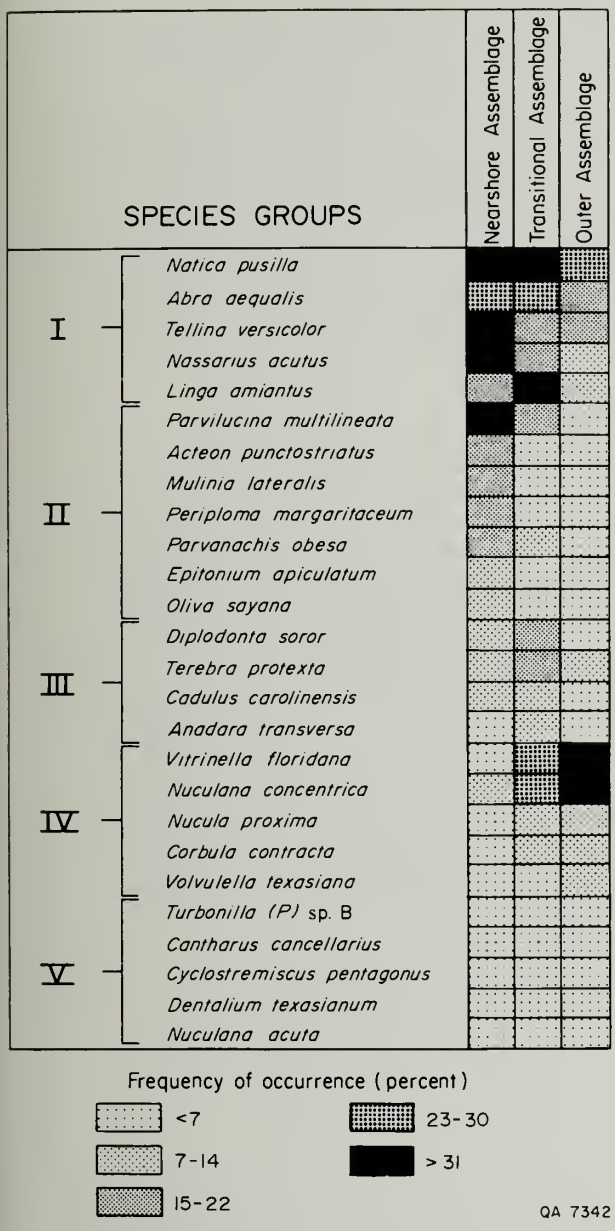


Figure 7

Frequency of occurrence of the most abundant mollusks according to the percentage of the total number of stations in each assemblage. Special groups are indicated by Roman numerals.

communities of shelled macrofauna south of the Mississippi River Delta and eight communities east of the delta. Faunal distribution south of the delta was closely correlated with water depth, bivalve feeding type, and substrate texture. East of the delta, faunal patterns reflected the nature of the water mass or distance from the delta front, water depth on the shelf away from the delta, and subdivision of the shelf by the Chandeleur-Breton Islands. DEFENBAUGH (1976) studied the benthic macroinvertebrates on the continental shelf of the northern Gulf of

Table 2

Characteristics of benthic faunal assemblages.

Assemblage	Total number of stations	Mean number of molluscan: Species per station	Mean number of molluscan: Individuals per station	Mean percent sand per station	Approximate depth range (m)
Nearshore	134	6	49	81	5.5–20.1
Transitional	263	5	14	43	4.3–27.4
Outer	157	3	5	28	5.5–29.3

Mexico primarily between Corpus Christi, Texas, and Pensacola, Florida, in a depth range of 59–600 ft (18–183 m). Based upon the results of his study and published and unpublished literature, Defenbaugh delineated an inner-shelf assemblage that occurred at depths of 13–66 ft (4–20 m) in soft mud, mixed sand and mud, or sand, and characteristic species included a large number of mollusks, such as *Nuculana concentrica* Say, 1824, *Anadara ovalis* (Bruguière, 1789), *Anadara transversa* (Say, 1822), *Noetia ponderosa* (Say, 1822), *Atrina serrata* (G. B. Sowerby, 1825), *Architectonica nobilis* (Röding, 1798), *Polinices duplicatus* (Say, 1822), *Anachis obesa* (C. B. Adams, 1845), and *Nassarius acutus* (Say, 1822). FLINT & RABALAIS (1981) delineated six station groupings of infaunal species, including a shallow-water group at depths of 33–89 ft (10–27 m), recovered from 25 collection sites (depths of 33–427 ft or 10–130 m) on the South Texas Outer Continental Shelf. The shallow-water group was found at four stations within the State-owned submerged-lands boundary. Molluscan species that made up more than 1% of the fauna in the shallow group included *Tellina versicolor* and *Anadara transversa*. HILL *et al.* (1982) delineated four assemblages in an area extending from Matagorda Peninsula in the north to the Rio Grande in the south and seaward to about the 656-ft (200-m) isobath. The 66-ft (20-m) isobath was the general inshore boundary. Three of the assemblages (two in the northern and one in the southern part of their study area) occurred within the State-owned submerged-lands boundary from the Brownsville-Harlingen to the Port Lavaca area.

Sediment Type and Molluscan Distributions

Sediments of the Texas inner shelf consist of gravel (shell), sand, and mud (silt and clay) (Figures 8, 9). The gravel-sized fraction is minor and is composed predominantly of shell and some rock fragments (MORTON & WINKER, 1979). The offshore extent of dominantly sand sediments varies greatly (MCGOWEN & MORTON, 1979). On the upper coast from Bolivar Roads to Sabine Pass, shelf sediments lack sand, and mud is the most extensive sediment (Figures 8a, b). Sand deposits are thin and limited to a narrow strip parallel to the beach and upper shoreface

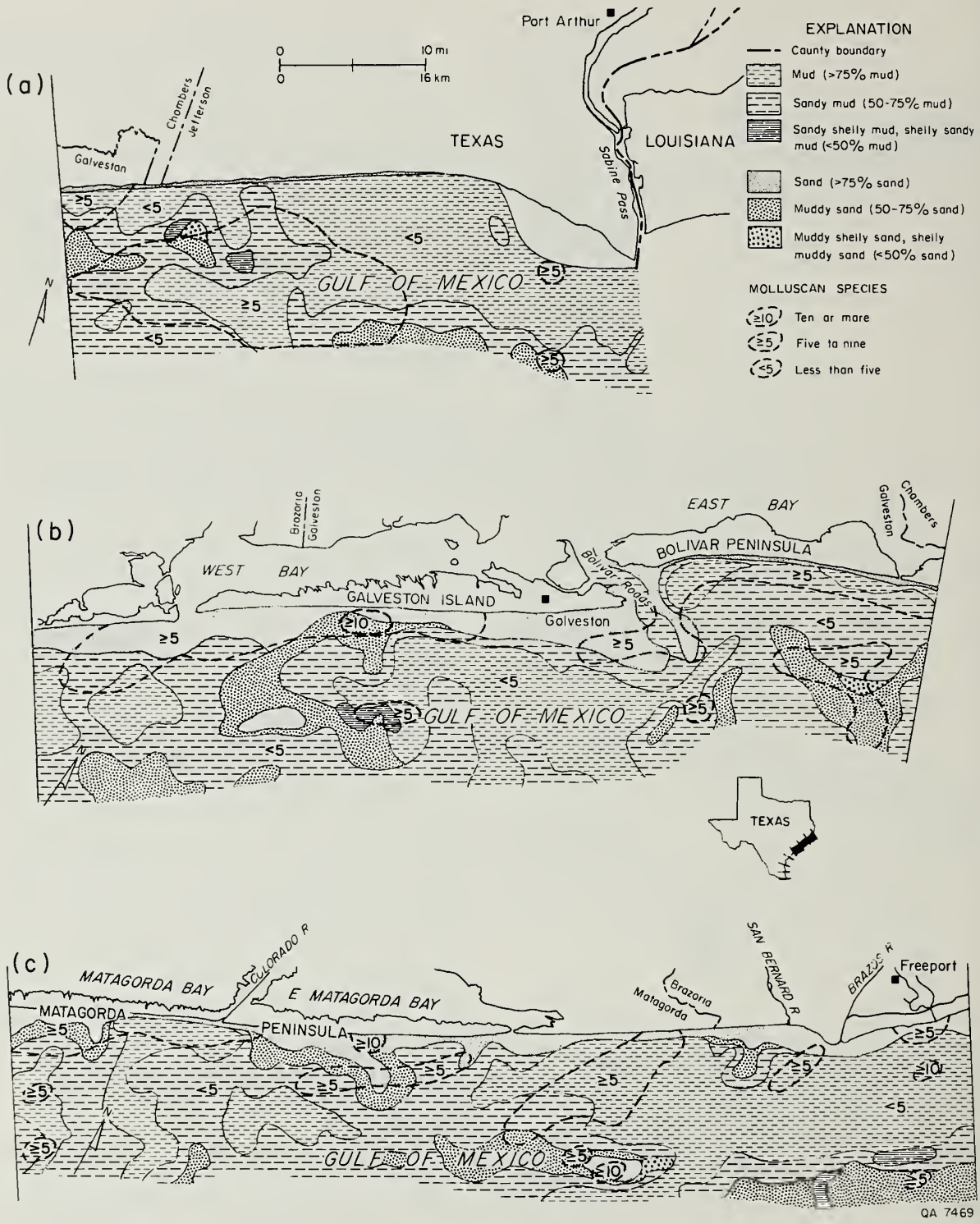


Figure 8

Distribution of gravel (shell), sand, and mud in the Beaumont-Port Arthur (a), Galveston-Houston (b), and Bay City-Freeport (c) areas (modified from WHITE *et al.*, 1985, 1987, 1988). Dashed lines delineate areas with similar numbers of molluscan species.

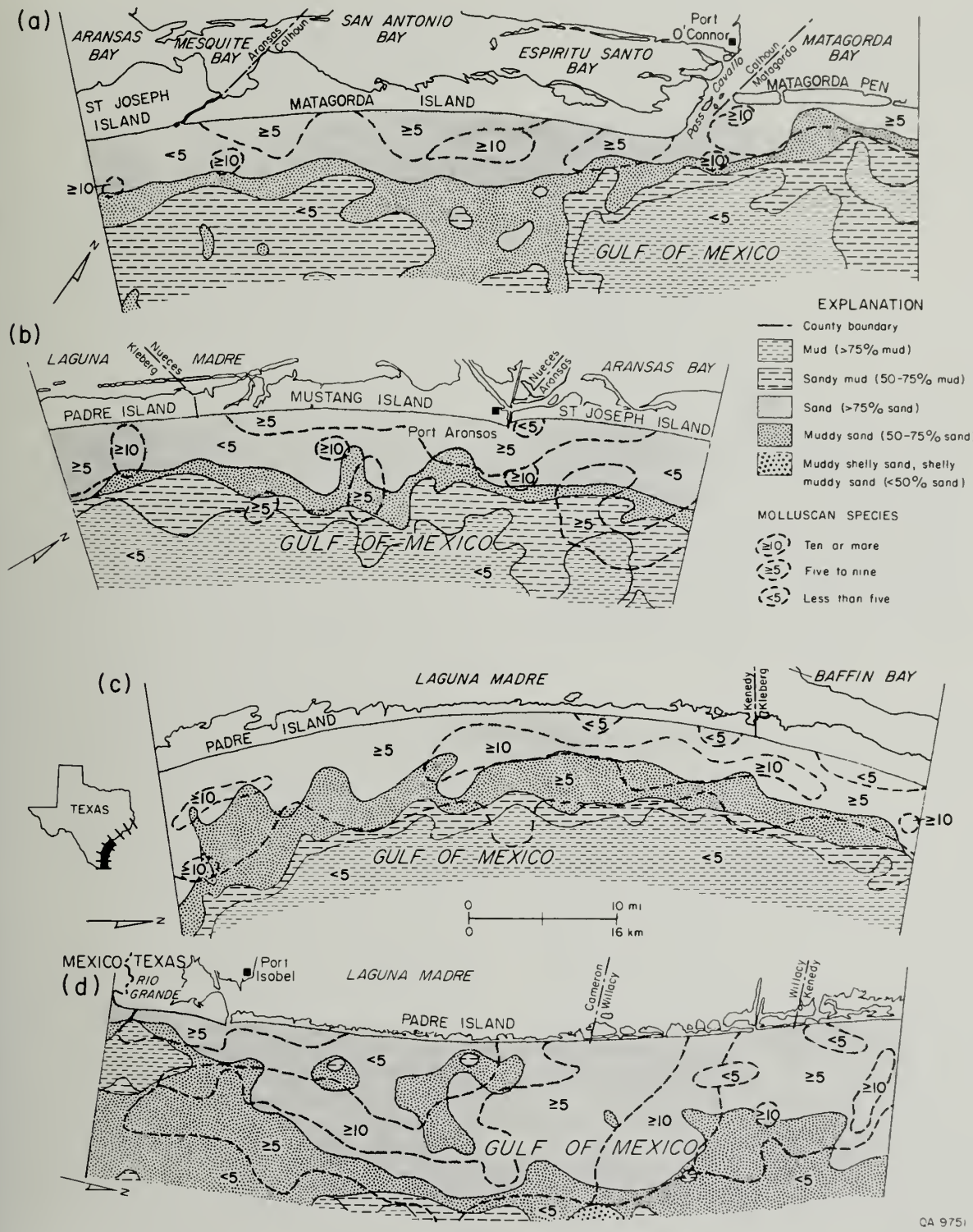


Figure 9

Distribution of gravel (shell), sand, and mud in the Port Lavaca (a), Corpus Christi (b), Kingsville (c), and Brownsville-Harlingen (d) areas (modified from WHITE *et al.*, 1983, 1986, in press, and unpublished data). Dashed lines delineate areas with similar numbers of molluscan species.

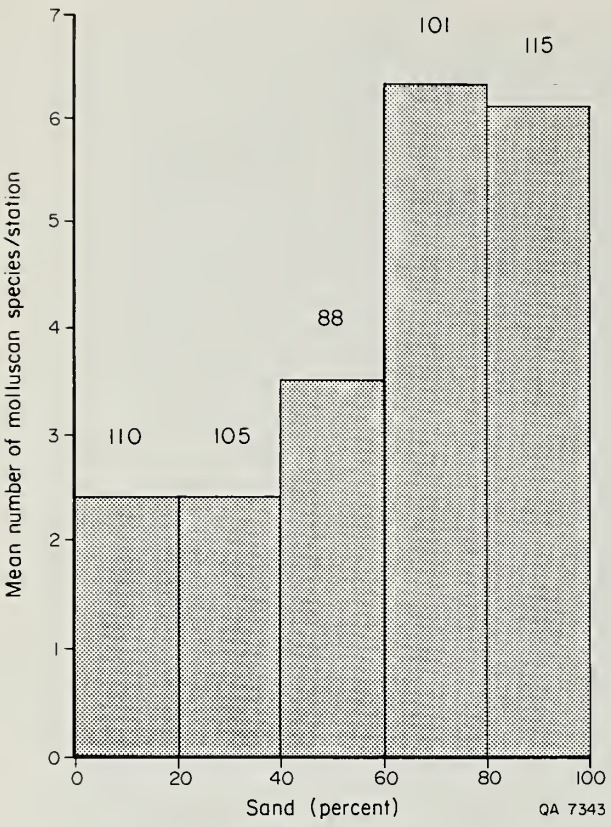


Figure 10

Mollusks and percent sand. Numbers above bars equal number of stations within that sediment type.

and generally less than 0.5 mile (0.8 km) from shore. Along Galveston Island in the Galveston-Houston area, sand extends 1 mile (1.6 km) offshore, where water depths are about 24 ft (7.3 m); just southwest of Bolivar Roads, sand extends up to 3 miles (4.8 km) offshore (Figure 8b). Grain size decreases offshore in the Galveston-Houston area, but less gradually than on the Port Lavaca and Corpus Christi inner shelf.

On the Corpus Christi inner shelf, sediment texture grades from sand through muddy sand and sandy mud to mud (McGowen & Morton, 1979) (Figure 9b). Bands of sand, muddy sand, sandy mud, and mud are oriented subparallel to the shoreline.

Sand and muddy sand dominate in the Brownsville-Harlingen area (White *et al.*, 1986) (Figure 9d). Sediments with high sand content (80 to 100%) are present from 1–9 miles (1.6–14.4 km) offshore. On the inner shelf in the Corpus Christi and Galveston-Houston areas, sand is not as abundant, and muds usually dominate at stations closer to shore.

More molluscan species are found in sand than mud. The mean number of species per station is highest in the 60–80%-sand range and lowest in the 0–40%-sand range (Figure 10). Most of the abundant mollusks occur primarily in sediments with high (80–100%) sand content (Table 3). Only *Nuculana concentrica* Say, 1824, *Vitrinella floridana* Pilsbry & McGinty, 1946, *Cyclostremiscus pentagonus* (Gabb, 1873), and *Volvulella texasiana* Harry, 1967, are most abundant in mud (0–20% sand). Eleven of the most abundant mollusks do not occur in mud, whereas only two species (*N. concentrica* and *V. texasiana*) are not present in sand.

Because more species are associated with sand than with mud, species numbers (species richness) at most stations in the Beaumont-Port Arthur area are lower and more uniform than at stations in the Galveston-Houston area, where sand is more prevalent. Also, the sandy zone along Galveston Island contains a nearshore assemblage, whereas there is no nearshore assemblage in the Beaumont-Port Arthur area. From Bolivar Roads to Sabine Pass, a transitional assemblage replaces the nearshore assemblage (Figures 5a, b).

The median and mean numbers of species per station in the Corpus Christi area increase with higher sand content and decrease with higher percentages of silt and clay (White *et al.*, 1983). This trend of higher species numbers (species richness) at sandy, nearshore stations is evident for all mollusks and both bivalves and gastropods. In the Kingsville area, numbers of species and individuals are generally highest at stations 1–5 miles (1.6–8.0 km) offshore that are characterized by sandy and muddy sand bottoms (60–100% sand) (White *et al.*, unpublished data).

The nearshore assemblage in the Corpus Christi and Kingsville areas generally follows the same trend as that of sediment with high (80 to 100%) sand content (Figures 6b, c, 9b, c). The mean percent sand for stations with a nearshore assemblage is 88% in the Corpus Christi area and 97% in the Kingsville area. The dominant sediment type for stations with a transitional assemblage is either muddy sand or sandy mud (20 to 60% sand). Muds (less than 20% sand) are predominant at stations with an outer assemblage.

In the Brownsville-Harlingen area, because sediments with high sand content are present up to 9 miles (14.4 km) offshore, more species are found farther offshore than in the Corpus Christi or Galveston-Houston areas (Figures 8b, 9b, d). Stations with any of the three assemblages in the Brownsville-Harlingen area are relatively sandy, averaging 92% in the nearshore assemblage, 70% in the transitional assemblage, and 53% in the outer assemblage.

Hill *et al.* (1982), too, found a significant correlation between the number of macrobenthic infaunal species and the amount of sand in the sediment. All the factors (number of species, number of individuals, and biomass) studied by Hill *et al.* (1982) on the South Texas shelf correlated best with high sand-to-mud ratios. A series of regression analyses showed that number of species, number of individuals, and biomass increased with increases in sand-to-mud ratios, the largest occurring where the sand-to-mud ratios exceeded 1.00.

Probably the primary factor accounting for the high

Table 3

Abundance and distribution of the most abundant mollusks.

Species	Total number of individuals	Percent of all (11,795) individuals	Total number of stations	Percent of all (554) stations	Predominant sediment type (% sand)	Predominant depth range (m)	Depth range (m)
Bivalvia							
Abra aequalis	4305	36.5	154	27.8	80–100	12.8–18.3	5.5–29.3
Tellina versicolor	621	5.3	148	26.7	80–100	9.1–11.0	3.7–27.4
Linga amiantus	462	3.9	136	24.5	60–80	14.6–18.3	5.5–29.3
Nuculana concentrica	412	3.5	133	24.0	0–40	11.0–12.8	3.7–29.3
Parvilucina multilineata	335	2.8	97	17.5	80–100	9.1–11.0 16.5–18.3	5.5–20.1
Diplodonta soror	236	2.0	65	11.7	60–80	16.5–18.3	5.5–25.6
Mysella planulata	204	1.7	8	1.4	80–100	16.5–18.3	3.7–25.6
Corbula contracta	137	1.2	58	10.5	60–80	12.8–14.6	9.1–29.3
Nucula proxima	106	0.9	56	10.1	60–80	14.6–18.3	9.1–29.3
Anadara transversa	79	0.7	36	6.5	60–80	18.3–20.1	3.7–25.6
Periploma margaritaceum	72	0.6	31	5.6	80–100	9.1–11.0	3.7–20.1
Strigilla mirabilis	62	0.5	17	3.1	80–100	14.6–16.5	9.1–20.1
Mulinia lateralis	57	0.5	29	5.2	80–100	5.5–11.0	3.7–12.8
Tellina iris	45	0.4	14	2.5	80–100	7.3–11.0	3.7–14.6
Solen viridis	30	0.3	20	3.6	80–100	12.8–14.6	7.3–23.8
Gastropoda							
Nassarius acutus	1261	10.7	134	24.2	80–100	9.1–11.0	3.7–20.1
Natica pusilla	552	4.8	232	41.9	80–100	11.0–18.3	3.7–29.3
Vitrinella floridana	406	3.4	121	21.8	0–40	16.5–20.1	5.5–29.3
Parvanachis obesa	239	2.0	83	15.0	80–100	11.0–14.6	5.5–20.1
Cyclostremella humilis	212	1.8	10	1.8	80–100	5.5–9.1	5.5–9.1
Terebra protexta	136	1.2	79	14.3	60–80	16.5–18.3	5.5–27.4
Cyclostremiscus pentagonus	111	0.9	29	5.2	20–40	11.0–12.8	9.1–29.3
Epitonium apiculatum	94	0.8	25	4.5	80–100	7.3–9.1	5.5–16.5
Acteon punctostriatus	93	0.8	52	9.4	80–100	12.8–14.6	3.7–27.4
Volvulella texasiana	58	0.5	46	8.3	0–20	12.8–16.5	9.1–29.3
Polinices duplicatus	42	0.4	29	5.2	80–100	9.1–11.0	5.5–20.1
Scaphopod							
Cadulus carolinensis	96	0.8	47	8.5	80–100	16.5–18.3	9.1–23.8
Dentalium texasianum	42	0.4	26	4.7	60–80	16.5–18.3	9.1–25.6
Dentalium eboreum	35	0.3	24	4.3	80–100	9.1–11.0	9.1–18.3

number of species (species richness) in predominantly muddy sand (60–80% sand) and sandy (80–100% sand) substrates is structural complexity or heterogeneity of the substrate. Coarse and heterogeneous sediments in sublittoral samples are generally more structurally complex and, seemingly as a result, have higher diversities than fine and homogeneous sediments (GRAY, 1974). For example, CRAIG & JONES (1966) found that, although species number does not necessarily correlate with diversity (GRAY, 1974), numbers of both epifaunal and infaunal species in the Irish Sea were highest in the coarsest sediments or gravel, followed by muddy sand, sand, and mud, in that order. In later studies, SANDERS (1968), BOESCH (1972), and GRAY (1974) substantiated the claim and noted that fauna on stable, sandy bottoms are generally more diverse than those on muddy bottoms because of the greater variety of microhabitats in coarser sediments.

Substrates of muddy sand may be better able to support benthic communities that are trophically more diverse than substrates with homogeneous muds or sands. The optimal substrate for both deposit and suspension feeders may be muddy sands or predominantly sandy substrates having an integral but smaller percentage of silt and clay. HARRY (1976) found that substrates with moderate amounts of silt and clay lend a certain rigidity to sandy substrates allowing the tunnels of burrowers to remain open. On the other hand, substrates with large amounts of clay and organic matter have reduced capillary circulation and increased chances of having anaerobic conditions (PURDY, 1964). And whereas deposit feeders have special feeding and respiratory adaptations to deal with these conditions, most suspension-feeding species cannot tolerate large amounts of silt and clay. Even small increases in the silt-clay content of substrates may clog interstitial spaces and

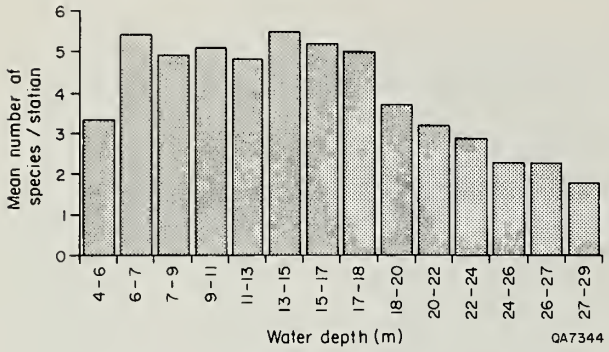


Figure 11

Distribution by depth (m) of the mean number of species per station.

slow oxygen diffusion to sediment depths (COULL, 1985). But aside from respiratory concerns, there are feeding problems, too. Sediments that consist predominantly of silts and clays are indicative of feeble currents that allow the fine particles to settle out; therefore, there is less food in the water column for suspension feeders (SANDERS, 1958).

Complete homogeneity of sand is not the ideal condition for high diversity either. Substrates in nearshore areas, where sand content may range from 90 to 100%, are unstable, and many benthic organisms are not suited to substrate mobility (PURDY, 1964). Additionally, substrates having greater than 90% sand have low total organic carbon values, and thus fewer deposit feeders that feed on the organics in the sediment will survive (PURDY, 1964).

Finally, biological interactions related to sediment distribution, such as trophic group amensalism, may also affect molluscan distribution. Suspension feeders may be unable to coexist with deposit feeders in muddy bottoms because of sediment instability produced by the deposit feeders. Such instability, termed "trophic group amensalism" (RHODES & YOUNG, 1970), inhibits suspension feeders and sessile epifauna by clogging filtering mechanisms, resuspending and burying larvae, and discouraging the settlement of larvae of suspension feeders and adults of sessile epifauna (RHODES & YOUNG, 1970). The reworked muddy surface is limiting to suspension feeders when the surface becomes mobile (RHODES & YOUNG, 1970).

Bathymetry and Molluscan Distributions

Shelf bathymetry near the Gulf of Mexico shoreline is characterized by a relatively steep slope, ranging from 6 ft/mile (1.8 m/km) near Sabine Pass in the Beaumont-Port Arthur area to 30 ft/mile (6 m/km) in the Brownsville-Harlingen area. The slope becomes more gradual beyond a distance of about 1 mile (1.6 km) offshore. At approximately 10 miles (16 km) offshore, the slope decreases, ranging from 1 ft/mile (0.2 m/km) in the Beaumont-Port Arthur area to 9–12 ft/mile (1.8–2.4 m/km) in the Brownsville-Harlingen area. Depths at stations 11 miles (17.6 km) offshore range from 40 ft (12.5 m) in the Beaumont-Port Arthur area to 96 ft (29.3 m) in the Brownsville-Harlingen area.

Analysis of the bathymetric distribution of all the mollusks sampled shows that the mean number of species per station is greatest in depths of 18–60 ft (6–18 m) (Figure 11). The mean number of species per station at this depth is 5.1, whereas the mean at stations at 60–96 ft (18–29 m) depths is 2.7. Mean numbers of species decrease from 5.0 to 1.8 as depth increases from 60 to 96 ft (18 to 29 m) (Figure 10). This decrease is similar to the decrease noted by PARKER (1960), in which the average number of macrobenthic species (primarily mollusks) decreased from 5.7 in his shallowest depth zone of 1–10 fathoms (2–18 m) to 1.0 in the next deepest zone of 10–20 fathoms (18–37 m). Both PARKER (1960) and HILL *et al.* (1982) found that the average number of macrobenthic species and individuals were highest at stations in their shallowest depth zones of 0–131 ft (0–40 m) and 1–10 fathoms (2–18 m), respectively.

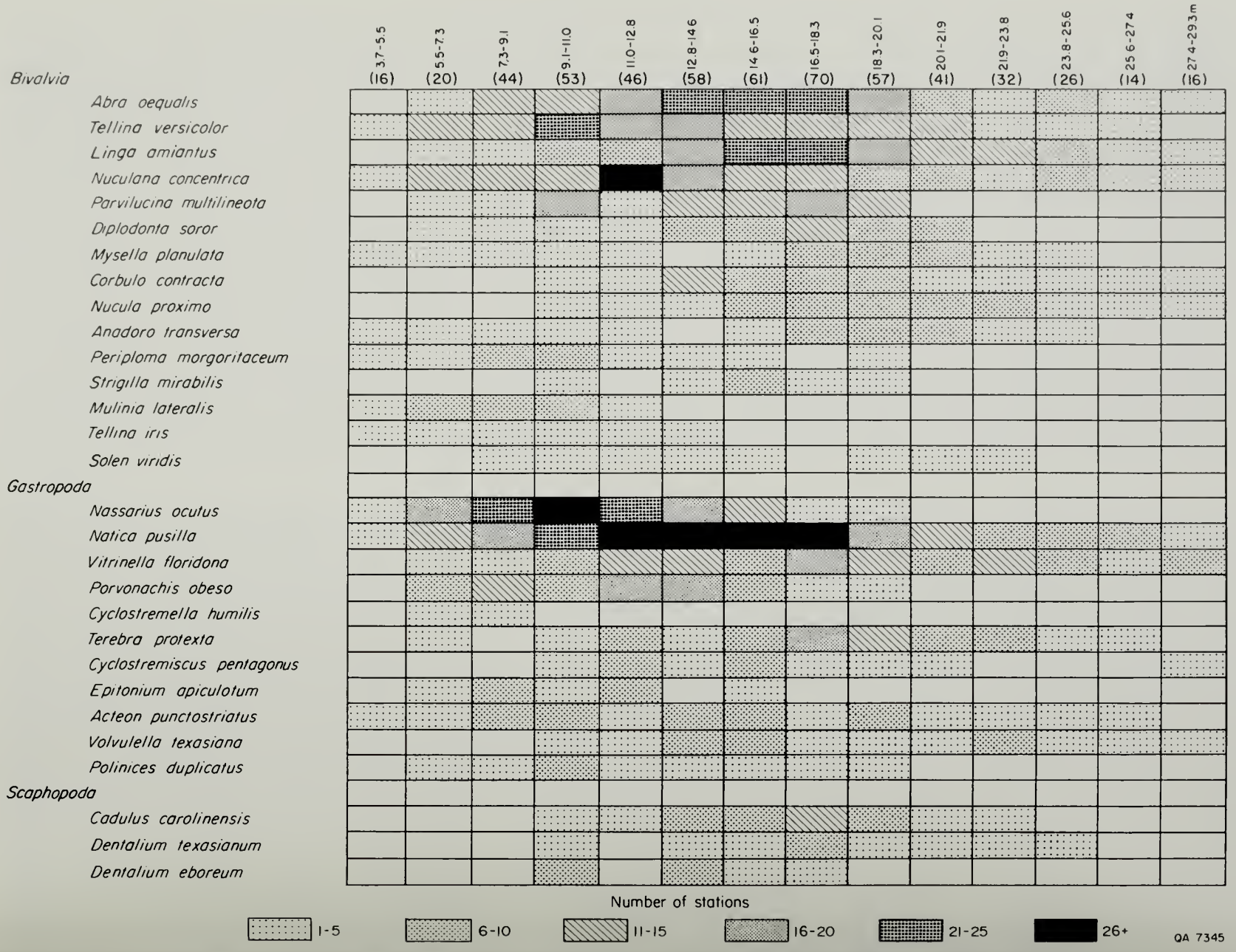
Many species are most abundant either at shallower-water stations (stations from 18.0–36.1 ft or 5.5–11.0 m deep) or deeper-water stations (stations from 47.9–60.0 ft or 14.6–18.3 m deep) (Figure 12). Species most abundant in shallower water include *Mulinia lateralis* (Say, 1822), *Periploma margaritaceum* (Lamarck, 1801), *Tellina iris* Say, 1822, *Tellina versicolor* DeKay, 1843, *Cyclostremella humilis* Bush, 1897, *Nassarius acutus* (Say, 1822), *Epitonium apiculatum* (Dall, 1899), and *Dentalium eboreum* Conrad, 1846. Those species most abundant in deeper water include *Mysella planulata* (Stimpson, 1857), *Nucula proxima* Say, 1822, *Anadara transversa* (Say, 1822), *Strigilla mirabilis* (Philippi, 1841), *Vitrinella floridana* Pilsbry & McGinty, 1946, *Terebra protexta* Conrad, 1845, and *Dentalium texasianum* Philippi, 1848. Many species that are most abundant in the shallower- or deeper-water group also occur at other depths; only *Nuculana concentrica* and *Natica pusilla* occurred at all depths (12.1–96.1 ft or 3.7–29.3 m) (Figure 12).

Some of the physical parameters that are related to water depth and that affect molluscan distributions are (1) sediment distribution; (2) nutrient availability (FLINT & RABALAIS, 1981); (3) turbidity (PARKER, 1960); (4) changes in bottom-water temperature (PARKER, 1960; HILL *et al.*, 1982); (4) oxygen levels (HILL *et al.*, 1982); and (5) hydrodynamic processes, such as the turbulence of water flow,

→

Figure 12

Distribution by depth (m) of the most abundant mollusks. Numbers in parentheses equal total number of stations within each depth range.


3.7-5.5 (16)
5.5-7.3 (20)
7.3-9.1 (44)
9.1-11.0 (53)
11.0-12.8 (46)
12.8-14.6 (58)
14.6-16.5 (61)
16.5-18.3 (70)
18.3-20.1 (57)
20.1-21.9 (41)
21.9-23.8 (32)
23.8-25.6 (26)
25.6-27.4 (14)
27.4-29.3m (16)
Bivalvia
Abra oequalis
Tellina versicolor
Linga amiantus
Nuculana concentrica
Parvilucina multilineota
Diplodonta soror
Mysella planulata
Corbulo contracta
Nucula proximo
Anadoro transversa
Periploma morgoritaceum
Strigilla mirabilis
Mulinia lateralis
Tellina iris
Solen viridis
Gastropoda
Nassarius ocutus
Natica pusilla
Vitrinella floridona
Porvonachis obeso
Cyclostremella humilis
Terebra protexta
Cyclostremiscus pentagonus
Epitonium apiculotum
Acteon punctostriatus
Volvulella texasiana
Polinices duplicatus
Scaphopoda
Cadulus carolinensis
Dentalium texasianum
Dentalium eboreum
Number of stations
1-5
6-10
11-15
16-20
21-25
26+
QA 7345

the settling velocities of sediment particles, and the transport of particles (SANDERS, 1958).

Sediment type and bathymetry are primary influences on molluscan distribution, but on the shallow inner shelf, extreme fluctuations in temperature and salinity are common and may be at least as significant to molluscan distribution as is substrate or bathymetry. Bottom-water temperatures on the inner shelf of the northwestern Gulf of Mexico and off the South Texas coast range from 14–16°C in the winter to 27–28°C in the summer (RABALAIS & BOESCH, 1987). Both PARKER (1960) and HILL *et al.* (1982) emphasized the effect of changes in bottom-water temperature on zonation of the infauna. PARKER (1960) noted that waters in the northern Gulf of Mexico in the 1- to 12-fathom (2- to 22-m) depth zone are constantly turbulent and virtually isothermal, and bottom temperatures are similar to the prevailing air temperatures. HILL *et al.* (1982) found that bottom-water temperatures on the South Texas shelf reflect seasonally changing temperatures to a depth of about 230–262 ft (70–80 m) and that infaunal assemblage boundaries correlate with the bottom of this seasonal water-temperature layer.

Salinities in near-shore waters range from open Gulf surface values of 36.4‰ to 20‰ or less after spring run-off or periods of high rainfall (FLINT & RABALAIS, 1981). Besides run-off from localized river discharges, freshwater discharges from the Mississippi and Atchafalaya rivers in Louisiana may produce reduced salinities in inner-shelf waters as far west as Galveston (RABALAIS & BOESCH, 1987). Reduced salinities in the late spring and increased nutrients may produce hypoxia in bottom waters in the summer. Hypoxic conditions may extend from off Louisiana to Freeport, Texas (HARPER *et al.*, 1981; RABALAIS & BOESCH, 1987).

Although physical parameters in the inner shelf environment are important in determining molluscan distribution, biological interactions, such as predation, may also play a major role. Predation by epibenthic fish, crabs, and shrimp, and by predatory infaunal organisms, such as polychaetes, nemerteans, crustaceans, and gastropods, have been shown to play significant roles in controlling the structure of many types of soft-bottom communities (REISE, 1984).

Predation pressures on mollusks in the predominantly muddy environment of the outer assemblage on the Texas inner shelf may be different than on mollusks in the sandier environments of the nearshore and transitional assemblages. Severe predation may decrease species diversity by reducing population densities of all species (VIRNSTEIN, 1977). However, low-level predation may enhance prey-species diversity by allowing less opportunistic species populations to enter the community and thus enhancing species richness. COULL (1985) studied meiofaunal abundance at a muddy and sandy site in North Inlet, South Carolina. COULL (1985) suggested that predation pressure on the meiofaunal community at the muddy site was much greater than on the community from the sandy site because (1) prey species occur closer to the surface at the muddy site giving potential predators easier access to their food, and (2) meiofaunal biomass was much greater in the mud-dwelling community; therefore, a predator would obtain much more energy from sorting 1 cm^3 of surface mud than 10 cm^3 of sand. However, COULL (1985) did not determine how predation affected the community structure of the mud-dwelling meiofaunal assemblage.

In summary, molluscan distribution seems to correlate highly with sedimentary and bathymetric patterns on the inner shelf of the Texas Gulf Coast. However, other physical and biological factors such as temperature, salinity, and predation are important and may be as significant to molluscan distribution as is substrate and bathymetry. Faunal-sediment associations indicate that more molluscan species occur in sand than in mud, and the most abundant species are found where the sand fraction is high. Analysis of the bathymetric distribution shows that the mean number of species is highest in a depth range of 18–60 ft (6–18 m), and that many species are most abundant at either shallower-water stations (stations from 18.0–36.1 ft or 5.5–11.0 m deep) or deeper-water stations (stations from 47.9–60.0 ft or 14.6–18.3 m deep).

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Vertical Size Gradients and Migratory Patterns of Two *Nerita* Species in the Northern Gulf of California

by

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Abstract. This study addresses patterns of vertical zonation, shell-size variation, and migratory behavior exhibited by two herbivorous intertidal gastropods in the northern Gulf of California, Sonora, Mexico. While actively foraging, *Nerita scabricosta* inhabited a zone from +3.1 m to +4.6 m above mean low water, whereas *Nerita funiculata* ranged from below +1.2 m to +4.6 m. Both species significantly increased in shell size with increasing tidal height. The size of *N. scabricosta* increased faster with tidal height than *N. funiculata.* In addition, *N. funiculata* increased faster with tidal height when inhabiting the zone of overlap with *N. scabricosta* than when in the non-overlap zone. When displaced up or down a tidal gradient, both species actively migrated in the direction of the habitat from which they were taken. This finding suggests that migratory behavior is in part responsible for the maintenance of interspecific zonation patterns.

INTRODUCTION

Many organisms exhibit striking patterns of vertical zonation in the rocky intertidal (CONNELL, 1961; RICKETTS *et al.,* 1985; NEWELL, 1970; STEPHENSON & STEPHENSON, 1972; LUBCHENCO, 1980; LEVINTON, 1982). Herbivorous gastropods are conspicuous members in many of these communities and often exhibit distinct zonation patterns. These patterns can be maintained by differential rates of growth and survival at various tidal heights, as well as through active migration (PAINE, 1969; VERMEIJ, 1972; BERTNESS, 1977; GENDRON, 1977; UNDERWOOD, 1979; LEVINTON, 1982; MCQUAID, 1982; DOERING & PHILLIPS, 1983; BOVBJERG, 1984).

Interspecific zonation patterns involve differing degrees of overlap between intertidal species, and range from sharp boundaries separating adjacent species to much less distinct gradations (UNDERWOOD, 1979; LEVINTON, 1982). Intraspecific zonation patterns usually involve shell-size variation along tidal gradients. For intertidal mollusks in general, VERMEIJ (1972) hypothesized that high-shore inhabitants tend to increase in shell size with increasing tidal height whereas lower-shore inhabitants tend to increase in shell size with decreasing tidal height.

Here I report on work conducted in the northern Gulf of California with two herbivorous archeogastropods, *Nerita funiculata* (Menke, 1851) and *Nerita scabricosta* (Lamarck, 1822) (Neritidae). Both species are found on rocky shores throughout the Gulf of California, and their geographic ranges extend to Peru and Equador, respectively (KEEN, 1971; ABBOTT, 1974; BRUSCA, 1980). In the northern Gulf of California, *N. scabricosta* occurs exclusively in the upper intertidal while *N. funiculata* inhabits the mid- and upper intertidal. Both species forage primarily during night low tides and remain inactive during high tides and daytime low tides (personal observations; see also LEVINGS & GARRITY, 1983).

The objectives of this study were to evaluate the zonation patterns exhibited by the two nerites. First, I documented the distribution of both species along a tidal gradient. Second, I determined intraspecific shell-size patterns along this gradient. Following VERMEIJ (1972), I predicted that both nerites would increase in shell size with increasing tidal height, as they are both upper-intertidal species. Third, using transplant experiments, I evaluated the role of migratory behavior in maintaining interspecific zonation patterns. If the two *Nerita* species maintain their distributions

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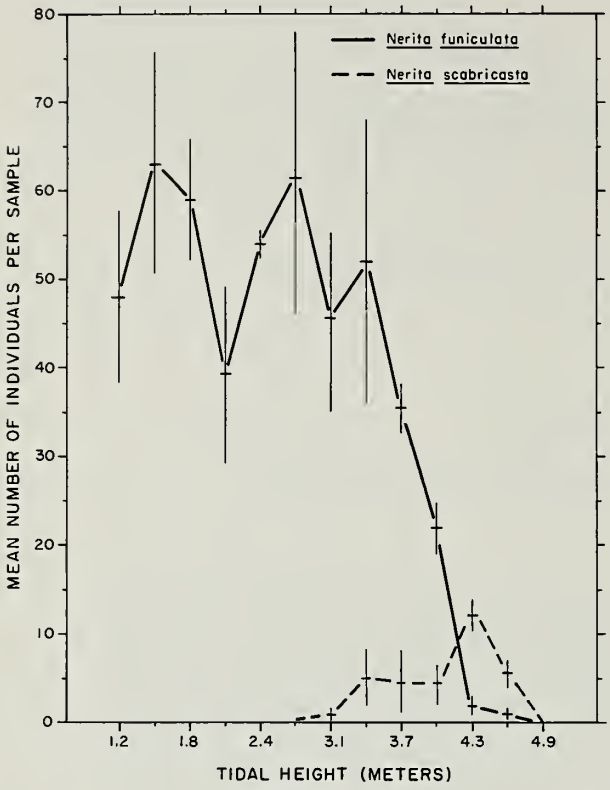

Figure 1

Mean number of *Nerita funiculata* and *N. scabricosta* per sample along a tidal-height gradient at Punta Peñasco, Sonora, Mexico (September 1983). Samples were taken during night low tides when both species were actively foraging. Vertical bars represent ±1 SE. Four samples per tidal height.

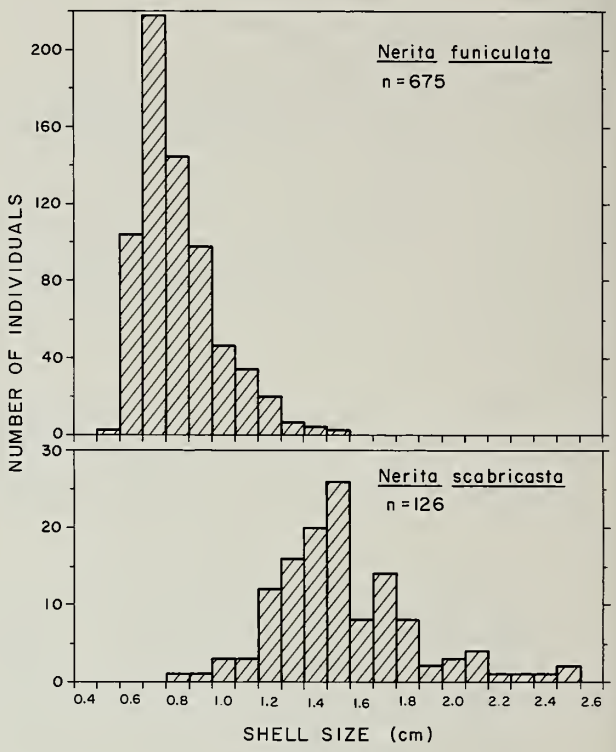

Figure 2

Shell-size distribution of *Nerita funiculata* and *N. scabricosta* at Punta Peñasco, Sonora, Mexico (September 1983).

through behavioral means, I predicted that downwardly displaced *Nerita scabricosta* and upwardly displaced *N. funiculata* should each migrate in the direction of the habitat from which they were taken, while control individuals should move smaller distances and in random directions.

MATERIALS AND METHODS

Normal foraging distributions of both species were determined by sampling at 0.3-m intervals along a vertical transect extending from +1.2 m to +4.9 m above mean low water. The transect, sampled in September 1983, was located in a steeply sloping basaltic boulder field at Punta Peñasco, Sonora, Mexico. Sampling procedure consisted of collecting all nerites from within a metal ring enclosing an area of 0.75 m^2. At each level, four replicate samples were taken at 1-m intervals along a horizontal line.

To evaluate shell-size patterns along this tidal gradient, I measured shell lengths (aperture to apex) with vernier calipers and generated linear regressions of tidal height against shell length for all collected individuals. I performed an analysis of covariance to determine if the two species exhibited significantly different regression-line slopes. With this same data set, I also generated a size-frequency distribution for both species.

To evaluate the hypothesis that rates of change in shell size with tidal height for *Nerita funiculata* were different in the zone of overlap with *N. scabricosta* (+3.1 to +4.6 m) than in the non-overlap zone (+1.2 to +2.8 m), I tested for equality of regression-line slopes in the two regions using an analysis of covariance.

Transplant experiments were initiated at Punta Peñasco during night low tides in November 1983. One hundred *Nerita funiculata* were collected from +1.2 m tidal height, marked with fluorescent paint, and randomly divided into equal control and experimental groups. The 50 controls were replaced at +1.2 m and the 50 experimentals were transplanted up to +4.3 m tidal height. A similar procedure was used with *N. scabricosta* except that the 100 individuals were collected from +4.3 m tidal height, controls were replaced at +4.3 m, and the experimentals were transplanted down to +1.2 m.

On the low tide of the following night, I returned to the study site and searched for the marked snails of both species. For all treatments, I recorded the distance and direction travelled by recaptured individuals of each species. For each snail, I converted migration vectors from polar to rectangular coordinates and, using Mann-Whitney tests, evaluated the following one-tailed hypotheses: (1) experimental *Nerita funiculata* moved significantly greater dis-

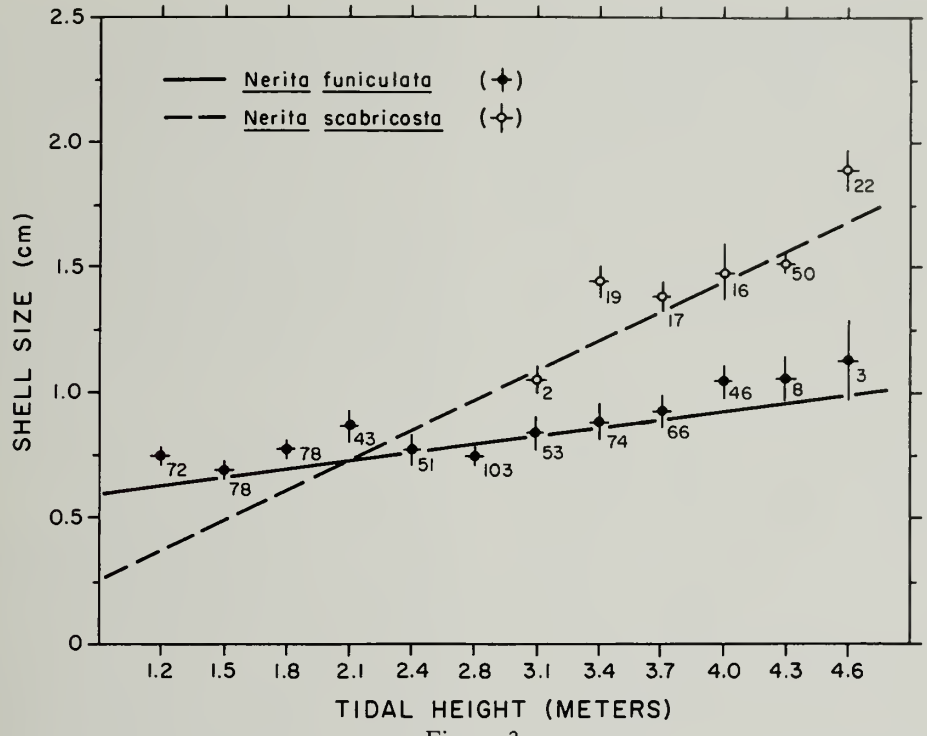

Figure 3

Linear regressions of mean shell size vs. tidal height for *Nerita funiculata* and *N. scabricosta* at Punta Peñasco, Sonora, Mexico (September 1983). Vertical bars represent ±1 SE.

tances downshore than controls, (2) experimental *N. scabricosta* moved significantly greater distances upshore than controls, and (3) experimental *N. scabricosta* moved significantly greater distances upshore than experimental *N. funiculata* moved downshore.

RESULTS

At Punta Peñasco, *Nerita scabricosta* inhabited a zone from +3.1 to +4.6 m above mean low water while *N. funiculata* occupied a zone from below +1.2 to +4.6 m (Figure 1; because of the tidal state, I sampled only as low as +1.2 m, but observed *N. funiculata* lower). Thus, the intertidal range of *N. scabricosta* was entirely contained within that of *N. funiculata*. *Nerita funiculata* was found in substantially higher overall densities than *N. scabricosta* (Figure 1) and was also noticeably smaller in size (Figure 2).

Both species exhibited a statistically significant increase in shell size with increasing tidal height (Figure 3; *Nerita scabricosta*, $n = 126$, $y = 0.279 + 0.312x$, $r = 0.428$, $P < 0.0001$; *N. funiculata*, $n = 675$, $y = 0.584 + 0.0928x$, $r = 0.502$, $P < 0.0001$). In addition, (1) the shell size of *N. scabricosta* increased at a significantly greater rate than that of *N. funiculata* (test for equality of slopes; $F = 35.03$, $P < 0.001$), and (2) the shell size of *N. funiculata* increased at a greater rate when in the zone of overlap with *N. scabricosta* than when in the non-overlap zone (test for equality of slopes; $F = 45.38$, $P < 0.001$).

For both species, experimental individuals moved significantly greater distances vertically (upshore or downshore) than the controls (Figure 4). Specifically, experimental *Nerita funiculata* moved downshore significantly more than controls ($P < 0.001$) whereas experimental *N. scabricosta* moved upshore significantly more than controls ($P < 0.001$). In addition, experimental *N. scabricosta* moved significantly greater distances upshore than experimental *N. funiculata* moved downshore ($P < 0.01$).

DISCUSSION

Nerita funiculata and *N. scabricosta* exhibit an overlapping pattern of vertical zonation on the intertidal basaltic boulder fields at Punta Peñasco. *Nerita scabricosta* inhabited the extreme upper intertidal and its range was contained entirely within that of *N. funiculata*. Throughout the intertidal zone, *N. funiculata* was substantially smaller than *N. scabricosta* and far more abundant. Both nerites also exhibited a significant increase in shell size with tidal height, thus supporting a prediction by VERMEIJ (1972) for upper-intertidal species. And lastly, when displaced up or down the tidal gradient, both species actively migrated in the direction of the habitat from which they were taken, thus suggesting that such behavior is in part responsible for the maintenance of interspecific zonation patterns.

Size-dependent zonation of intertidal gastropods has been described for many herbivorous and carnivorous species

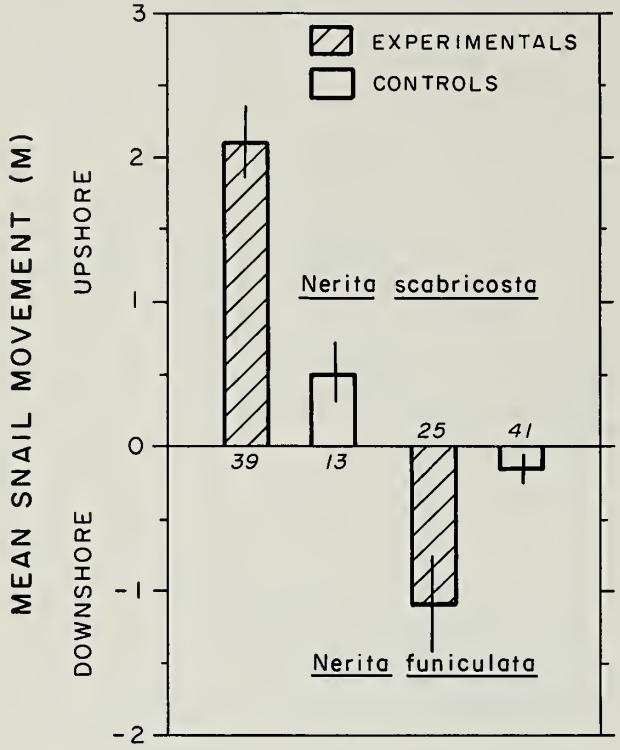

Figure 4

Mean upshore and downshore movements of marked *Nerita funiculata* and *N. scabricosta* (November 1983). The number of recaptured individuals (out of a possible 50) is listed for each mean. Vertical bars represent ±1 SE.

(Bakkar, 1959; Frank, 1965; Edwards, 1969; Paine, 1969; Sutherland, 1970; Vermeij, 1972; Coombs, 1973; Chow, 1975; Bertness, 1977; Markowitz, 1980; McQuaid, 1982). With the exception of Bakkar (1959) and McQuaid (1982), these studies have supported Vermeij's (1972) prediction that upper-intertidal mollusks increase in shell size with increasing tidal height whereas lower-intertidal species decrease in shell size with increasing tidal height.

Numerous factors may explain the patterns of intra- and interspecific shell-size variation observed in this study. First, owing to the effects of surface-to-volume ratios, desiccation tolerance usually increases with increasing size of individual gastropods. In most cases, this relationship applies to both within- and between-species comparisons (see review by Underwood, 1979). Thus, the results reported here are consistent with the hypothesis that surface-to-volume ratios explain the two intraspecific shell-size gradients. Second, Vermeij (1978) has noted that *Nerita scabricosta* can hold extravisceral water in its nonpartitioned shell while *N. funiculata* does not have this ability. Further, Garrity (1984) showed that larger *N. scabricosta* hold proportionately more water than smaller individuals. These observations suggest that *N. scabricosta* may acquire a two-fold benefit from increases in shell size: (1) surface-to-volume ratio effects and (2) extravisceral water effects. This double benefit may explain why the regression-line slope for *N. scabricosta* was significantly steeper than for *N. funiculata*; increases in body size are more valuable to *N. scabricosta* in combating environmental stress.

The significantly greater rate of increase in shell size for *Nerita funiculata* when co-occurring with *N. scabricosta* (+3.1 to +4.6 m; Figures 1, 3) may have resulted from interspecific competition. Perhaps larger *N. funiculata* are better able to compete with *N. scabricosta* than are smaller individuals. If this were the case, selection would favor the presence of larger *N. funiculata* in the overlap zone. Alternatively, water loss may be more pronounced in the upper intertidal such that only larger individuals can survive there. Thus, what appears to be a pattern suggesting interspecific interactions may actually result from variation in physiological tolerances to stress.

The transplant experiments indicate that both nerites must be able to (1) recognize their preferred habitat, (2) correctly assess the direction of this habitat when they have been displaced or when environmental conditions change, and (3) move in the direction of this region (Figure 4). Such behaviors can result from the ability of gastropods to respond to various environmental cues, such as gravity, light, water pressure, or inundation-exposure period (see review by Underwood, 1979).

In this study, downwardly displaced *Nerita scabricosta* showed stronger migratory tendencies than did upwardly displaced *N. funiculata*. The apparent difference in migration rates may have resulted from a stimulus difference; the transplanted *N. scabricosta* were moved completely outside their normal range and exposed to substantially longer periods of submersion, while the transplanted *N. funiculata* were moved only to the upper portion of their normal range (movement completely outside of their normal upper limits would have put them in an area outside of the splash zone). Thus, the environmental changes brought about by the transplants may have been greater for *N. scabricosta* than for *N. funiculata* and, as a consequence, the former tended to migrate greater distances. Alternatively, the observed difference in rates of movement could be due to the fact that transplanted *N. scabricosta* were significantly larger than transplanted *N. funiculata* and larger individuals can move greater distances. Supporting this contention is the work of Levings & Garrity (1983) and Garrity & Levings (1984) which document that the distance traveled by *N. scabricosta* increases with shell size.

In conclusion, this study has revealed numerous ways in which the ecology of *Nerita* in the northern Gulf of California differs from that reported for the two species in Panama (Garrity & Levings, 1981; Levings & Garrity, 1983). First, *N. funiculata* is far more abundant than *N. scabricosta* in the northern Gulf, whereas the reverse is true in Panama. Second, *N. scabricosta* does not forage over as wide a vertical range in the northern Gulf as it does in Panama. And third, *N. funiculata* commonly occurs in unprotected microhabitats while inactive in the

northern Gulf whereas it is restricted to crevices in Panama. This latter difference may be due to comparatively greater fish predation in the tropics (see BERTNESS *et al.*, 1981; GARRITY & LEVINGS, 1981).

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Octopodid Paralarvae from Hawaiian Waters

by

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Abstract. Thirteen types of octopodid paralarvae are recognized from Hawaiian waters, although the adults of only seven species (three are undescribed) are currently known from this area. The most common 11 paralarval types are described; five types can be identified with known adults. Stage II paralarvae differ from Stage I paralarvae by the presence of sucker buds on their arms. The number of suckers in Stage I paralarvae is characteristic for a species, as are their chromatophore patterns. Hatchlings have a high density of integumental pores containing secretory granules that may produce a mucous "drogue" to assist in offshore transport.

INTRODUCTION

The octopodid fauna of Hawaii is poorly known although several species are of economic importance. There has not been a recent review or modern systematic treatment of the group as a whole, and references are few and widely scattered in the literature. SOULEYET (1852) briefly described *Octopus hawaiiensis* in a report of the French *Bonite* expedition. In the same year, GOULD (1852) described and figured *O. ornatus* which had been collected by the U.S. Exploring Expedition. In 1885, HOYLE (see also 1886) described *O. marmoratus* (subsequently synonymized with *O. cyanea* by ROBSON [1929]) from material obtained by the *H.M.S. Challenger* expedition. BERRY (1909) briefly diagnosed *Polypus hoylei* (subsequently placed in the genus *Berrya* by ADAM [1939]) and in 1913, BERRY described *Scaeurgus patagiatus* (subsequently placed in the synonymy of *S. unicirrus* by ROBSON [1929] and by VOSS [1951] but reinstated by TOLL [1988]). In his monograph, BERRY (1914) expanded the documentation of Hawaiian cephalopods, treating all the species recognized at that time. With the exception of a few records listed by BOONE (1938) and VOSS' (1981) review of *O. ornatus,* no other systematic work has been done on Hawaiian octopodids. Several species of *Octopus* not included in the above works, however, are in our collections from Hawaii.

At present the adults of seven species of octopodids are recognized from Hawaii. Four are named, *Octopus cyanea, O. ornatus, Berrya hoylei* and *Scaeurgus patagiatus.* (*Octopus hawaiiensis* has not been reported since its original description and its identity remains uncertain.) Three species are unnamed. One (our Type E) is a shallow-water and intertidal species whose activity pattern was discussed by HOUCK (1977, 1982). Another (our Type I) has permanent flattened tubercles and a low lateral keel on the mantle. This species is commonly captured in trawls by shrimp fishermen (Van Heukelem, University of Maryland, personal communication). A third is a large species, captured on two occasions by fishermen from depths of about 700 m, and is similar in appearance to the giant octopus of the North Pacific, *O. dofleini.* Immature ovarian eggs are 17 mm long indicating the absence of a planktonic stage.

The habits of octopod hatchlings depend greatly on the size of the egg. In most species with small eggs (<4 mm long) the young are planktonic (*i.e.,* they are paralarvae—see YOUNG & HARMAN, 1988) for unknown lengths of time. Five of the seven known Hawaiian octopods lay small eggs. An additional species produces large eggs. The egg size of the one other species is unknown.

The first thorough descriptions of the development of paralarval stages of octopodids were given by NAEF (1923,

1928). At present, only a few species have been studied in detail, even though observations and figures are scattered throughout the literature (see HOCHBERG *et al.*, in press). While no previous studies have examined the paralarvae of Hawaiian octopodids, several figures and photographs of unidentified advanced paralarvae have been published (BERRY, 1914; BOWER, 1981; NEWBERT, 1984).

In this paper, we examine only the Stage I paralarvae. These paralarvae appeared to be sampled quantitatively by our plankton nets while older stages were not. In addition, since the duration of Stage I must be relatively short, we can be assured that all Stage I paralarvae hatched in Hawaiian waters.

MATERIALS AND METHODS

Specimens were obtained from plankton tows taken from both the windward and leeward sides of the island of Oahu and from the windward side of the island of Hawaii. Tows were taken during all seasons and over a period from 1982 to 1987. Nets used were: 1-m ring net, 70-cm Bongo net, 4-m^2 square-frame net, and a 4-m^2 ring net. Net mesh sizes were 333 or 505 μm. The approximately 550 tows filtered more than 2.5×10^6 m^3 of water. Some tows were taken at discrete depths, but most were oblique and fished from 200 or 300 m to the surface. All of the octopodid paralarvae collected were identified. A small proportion of these were used to provide the following descriptions and measurements.

Net-captured material was fixed in 4–5% seawater formalin and subsequently transferred to 40% isopropyl alcohol. Fading of chromatophores occurred in some cases but, in general, fading was not a serious problem. Calcareous sand grains were added to the samples to buffer the alcohol solution. Live eggs of *Octopus cyanea* were obtained from an octopus that had spawned in the Waikiki Aquarium. These were raised through hatching. Preserved eggs and hatchlings of a few other species were obtained from other workers. In a few cases we attempted to rear paralarvae taken from the plankton.

Voucher specimens of all figured species are deposited at the Santa Barbara Museum of Natural History (SBMNH). The remaining material is deposited at the University of Hawaii.

TERMINOLOGY

Where possible we have used the terminology recommended by the Cephalopod International Advisory Council handbook on the identification of young cephalopods (see HOCHBERG *et al.*, in press).

Stage I Paralarva—The stage between hatching and the development of sucker buds on the arms. Hatchlings have a fixed number of fully formed arm suckers but no sucker buds. Considerable growth occurs before sucker buds begin to appear on the arms. The presence of clearly defined sucker buds (Figure 1B) marks the end of this stage and the beginning of Stage II. In lieu of data on the complexities of later development, we consider Stage II to extend through settling and metamorphosis.

Measurements:

Mantle Length (ML)—Length from the most posterior point of the mantle to the most anterior point of the mantle margin measured along the dorsal midline. This definition differs from the standard definition. In paralarvae, unlike adult octopodids, the mantle muscle at the head-mantle fusion is easily seen and accurate measurements can be made. The modified definition applies to all paralarvae measured.

Head Width—Width measured dorsally across the head at the level of the center of the eyes.

Eye Diameter—Anterior-posterior length of the eyeball measured dorsally.

Arm Length—Length of the arm from the center of the mouth to the distal tip of the arm. Since the arms are usually equal in length the measurement of any arm is satisfactory. Often a specific arm cannot be measured owing to its small size (the arms cannot be straightened).

Arm Length Formula—Relative length of the arms beginning with the longest. For example: 3 > 2 > 1 > 4.

Arm Sucker Formula—Relative diameter of the suckers beginning with the largest. Suckers are numbered beginning nearest the mouth.

Indices—Ratio of a given measurement to the mantle length of the same specimen.

Chromatophores (types):

Tegumental—Chromatophores lying in or near the integument. These can be of two types: *superficial* chromatophores of the integument on the exposed outer surfaces of the octopus or *supravisceral* chromatophores of the integument dorsal to the viscera but within the mantle cavity.

Extrategumental—Chromatophores lying in connective tissue well beneath the outermost integument. In the species discussed, this category includes the following chromatophore fields: Dorsal Head, Dorsal Eye and Ventral Head. The separation of the Extrategumental and Tegumental chromatophores becomes arbitrary near the base of the arms.

Chromatophore fields (Figure 2):

Dorsal Arm; Ventral Arm—Chromatophores on the aboral surfaces of each arm of the dorsal or ventral pair of arms. These are commonly in either one or two series (=rows).

Arm Base—A distinctive enlarged chromatophore lying at the aboral base of the arm. Counts given in the description are the total from all arms.

Ventral Mantle, Anterior Margin—Chromatophores lying along or near the anterior margin of the ventral mantle.

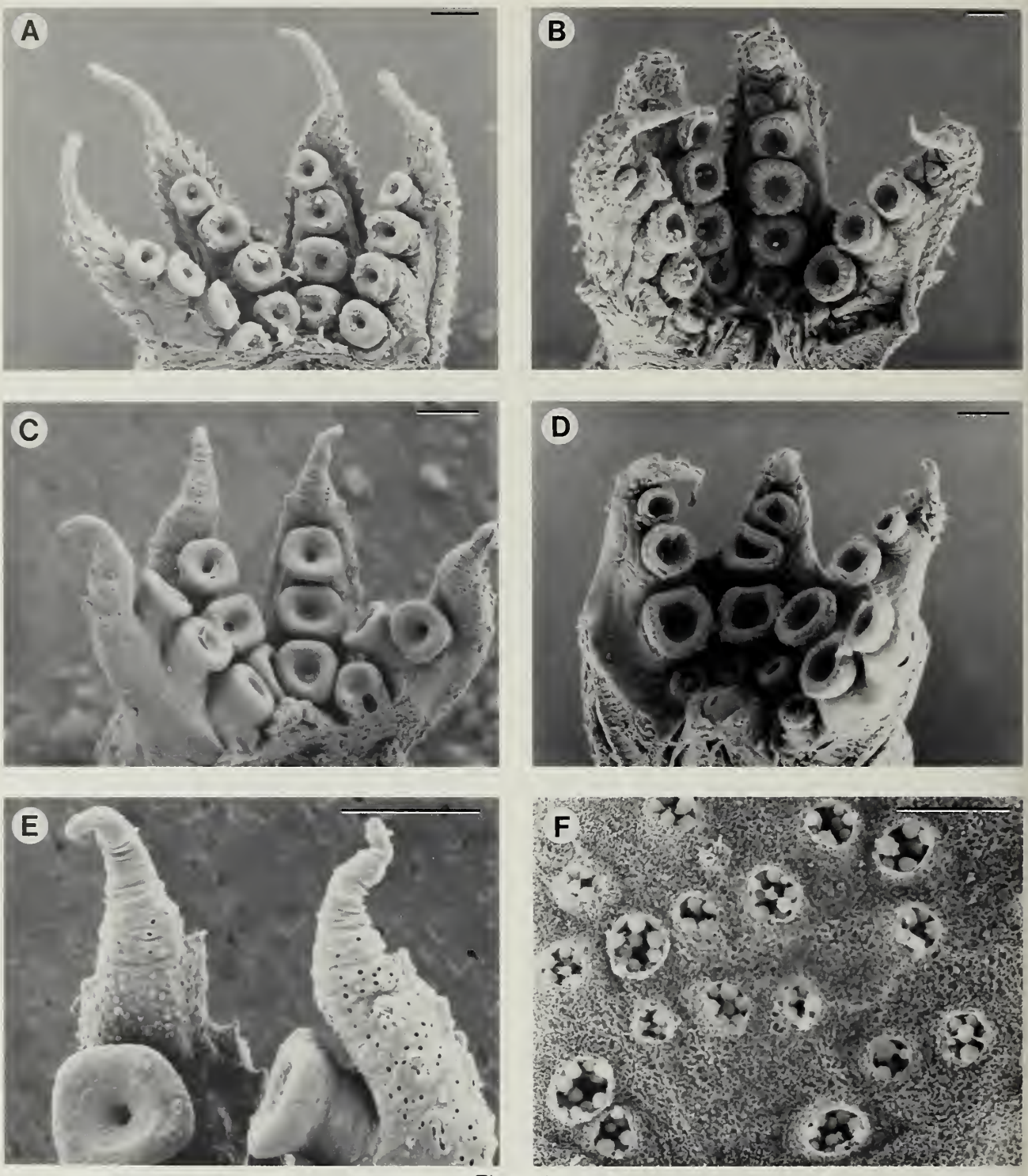


Figure 1

A. Oral view of arms of Type E paralarva (hatchling, 1.6 mm ML) showing four suckers. B. Oral view of arms of early Stage II paralarva of Type E (2.0 mm ML) showing development of sucker buds. C. Oral view of *Octopus cyanea* paralarva (hatchling, 1.2 mm ML) showing three arm suckers. D. Oral view of Type I paralarva (1.2 mm ML) showing relative sucker sizes. E. Arm tips of *O. cyanea* hatchling showing pores on arm surfaces; many of the pores are plugged by secretory products and appear only as rough spots. F. Oral surface of arm of *O. cyanea* hatchling showing high magnification of pores and included secretory spherules. Scale bars: A–E = 0.1 mm, F = 0.01 mm.

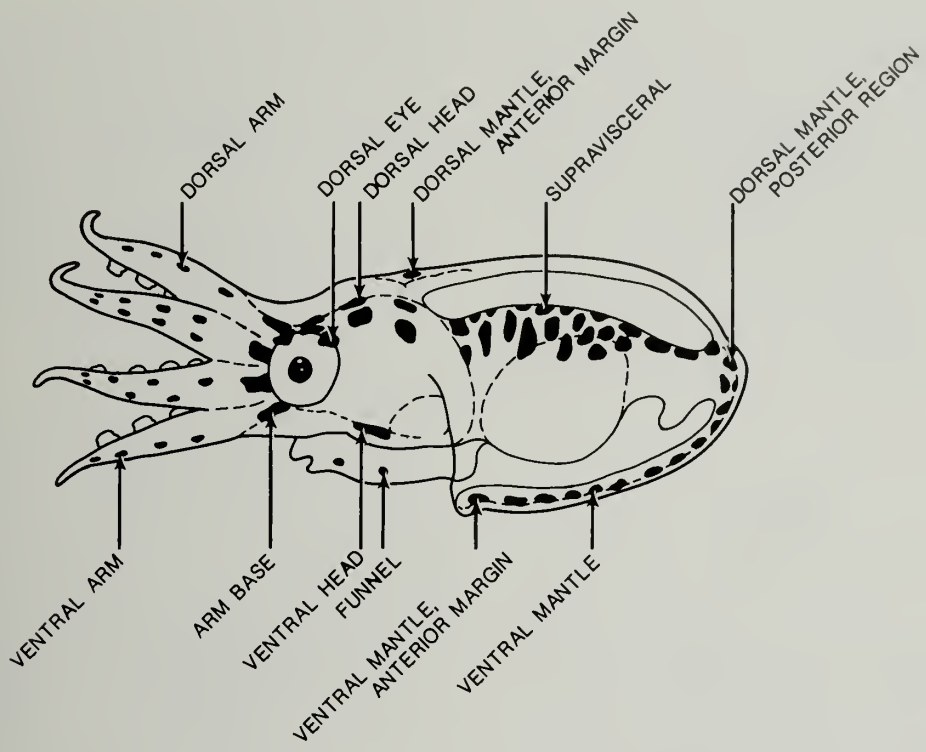


Figure 2

Lateral view of hypothetical Stage I octopodid paralarva illustrating chromatophore fields.

Ventral Mantle, Anterior Region—Chromatophores on the anterior third of the ventral mantle, excluding those of the anterior margin.

Ventral Mantle, Midregion—Chromatophores on the middle third of the mantle measured in the anterior–posterior direction.

Ventral Mantle, Posterior Region—Chromatophores on the posterior third of the ventral mantle.

Posterior Cap—Chromatophores on the posterior dome of the mantle only when they are present in isolation from other mantle regions. In most cases the posterior dome includes chromatophores from the Ventral Mantle, Posterior Region and/or the Dorsal Mantle, Posterior Region.

Dorsal Mantle, Anterior Margin—Discrete band of chromatophores lying along or near the anterior margin of the dorsal mantle muscle.

Dorsal Mantle, Anterior Region—Chromatophores on the anterior third of the dorsal mantle, excluding those of the anterior margin.

Dorsal Mantle, Posterior Region—Chromatophores at the posterior tip of the dorsal mantle. These chromatophores usually are part of a continuous patch that includes chromatophores of the Ventral Mantle regions.

Funnel—Chromatophores on the ventral surface of the funnel. These are counted in groups beginning at the anterior end of the funnel. Thus, 3+2 would mean 3 chromatophores in an anterior band on the anterior tip of the funnel and 2 chromatophores in a band more posteriorly.

Dorsal Head—Deep chromatophores in the connective tissue covering the musculature of the head dorsally. Often the more-posterior chromatophores are partially or completely covered by the dorsal mantle muscle. Chromatophores are counted according to their position on the head from anterior to posterior positions. For example, a 2+4+4 count means 2 anterior chromatophores in a transverse series, 4 intermediate chromatophores in a transverse series, and 4 posterior ones in a transverse series.

Dorsal Eye—Chromatophores lying on the dorsal surface of the eye, occasionally extending partially (well less than half the chromatophore) into the region of the Dorsal Head chromatophores. Often difficult to see against the dark pigment of the eye and can be confused with Dorsal Head chromatophores but are separable by the above definition.

Ventral Head—Deep chromatophores lying on the ventral head musculature.

Supravisceral—Chromatophores mostly in the dorsal integument covering the viscera within the mantle cavity.

Chromatophore arrangements:

Simple band—Transverse series of chromatophores in a single line.

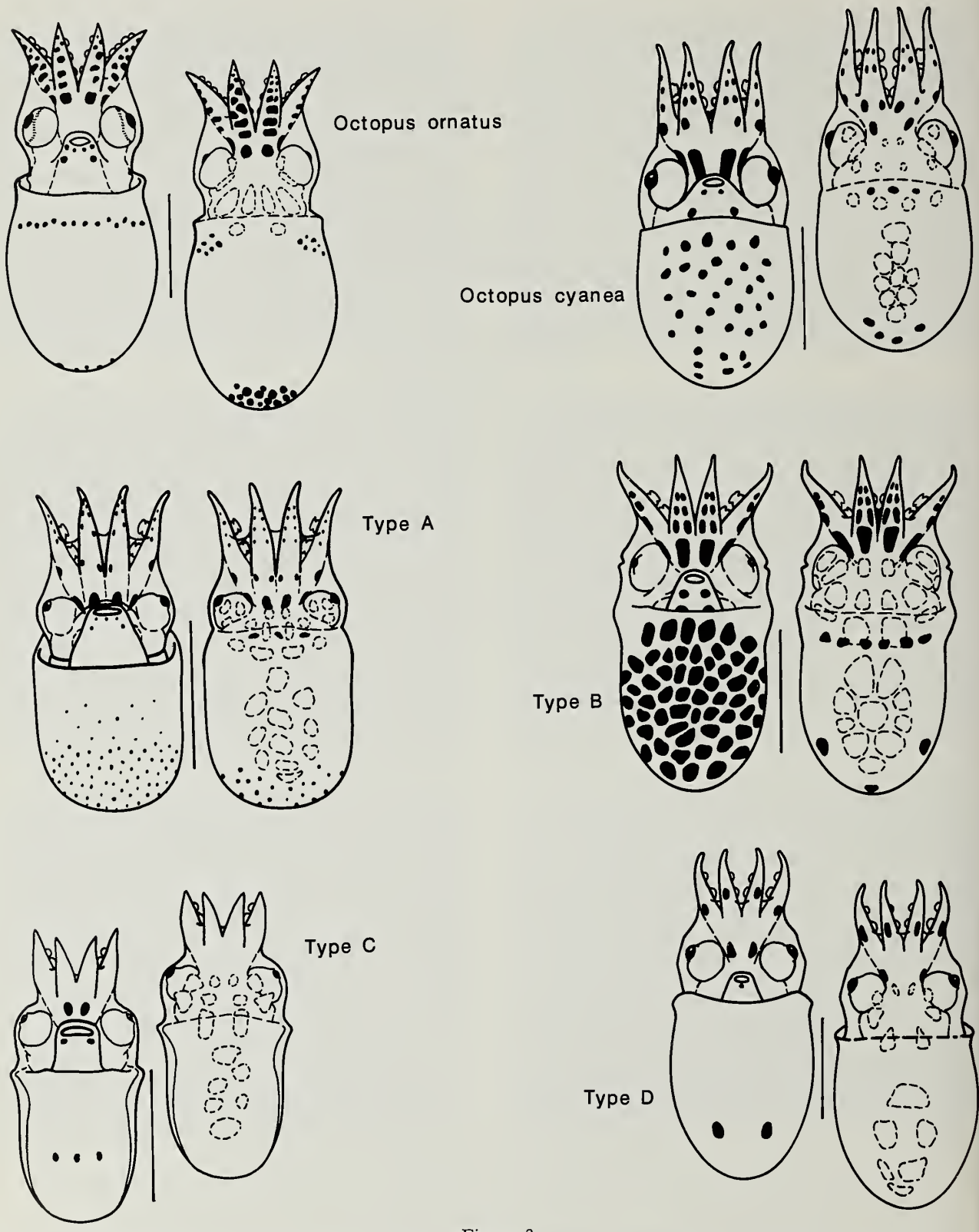


Figure 3

Dorsal and ventral views of Stage I octopodid paralarvae with seven (*Octopus ornatus*) or three (*O. cyanea* and Types A–D) suckers per arm. Scale bar = 1 mm.

Complex band—Transverse series of chromatophores in a single, very irregular line or many (regular or irregular) lines.

Complex stripe—Longitudinal series of chromatophores in a single, very irregular line or many (regular or irregular) lines.

Chromatophore counts:

Mantle, number across—Number of chromatophores across the ventral surface of the mantle. Usually counted in an arbitrary zig-zag line since chromatophores may not be perfectly aligned.

RESULTS

Most measurements of Stage I paralarvae are presented as ranges and indices. Where species change shape considerably over the size range measured, indices (measurement as a fraction of the mantle length) are more useful. Indices are given in parentheses and include the minimum values, the mean (in italics) and the maximum value. Generally, when chromatophores in a particular field are absent, the field is not listed. Occasionally, however, the absence is deemed unusual and the group is listed with a count of zero.

Species Descriptions of Paralarvae

Octopus ornatus

(Figure 3)

Material examined: 23 specimens: 1.9–3.6 mm ML. Voucher SBMNH 35115 (3 specimens).

Body proportions: Mantle Length: 1.85–2.4 mm; Head Width: 1.0–1.6 mm (0.74–*0.82*–0.95); Eye Diameter: 0.3–0.5 mm (0.23–*0.28*–0.33); Arm Length: 0.48–0.80 mm (0.37–*0.42*–0.48); Arm Length Formula: subequal.

Suckers: Number per arm: 7; Largest diameter: 0.14–0.16 mm (0.06–*0.08*–0.09); Smallest diameter: 0.06–0.08 mm (0.03–*0.03*–0.05); Sucker Diameter Formula: $2 = 3 > 1 = 4 > 5 > 6 > 7$, $1 = 2 = 3 > 4 > 5 > 6 > 7$ or $2 > 1 > 3 \geq 4 > 5 > 6 > 7$.

Tegumental chromatophores: Dorsal Arms: one series proximally becoming two distally; Ventral Arms: irregular series proximally, two series distally; Arm Base: 8; Funnel: 5–9 scattered near orifice; Posterior Cap: 20–26 in smallest specimens; Ventral Mantle, Anterior Region: 10–14 across in simple to complex band. Dorsal Mantle, Anterior Region: See **Remarks**; Supravisceral: 8–13 (not shown in figure).

Extrategumental chromatophores: Dorsal Head: 4+2; Dorsal Eye: 3/eye, occasionally 2 or 4/eye; Ventral Head: 0.

Remarks: This species' chromatophore patterns bear little resemblance to those of other species examined here. Chromatophore numbers in nearly all chromatophore fields increase as size increases. In the smallest specimens there are no Dorsal Mantle, Anterior Margin chromatophores. At larger sizes, the simple band of the Ventral Mantle, Anterior Margin field (see Figure 2) becomes complex, broadens and extends dorsally to eventually encircle the mantle near the end of Stage I. Concurrently, chromatophores appear on the Dorsal Mantle, Anterior Margin and, subsequently, extend over the head as size increases. The supravisceral chromatophores are difficult to detect through the mantle. Stage I terminates between 3.0 and 3.2 mm ML.

We have obtained eggs of *Octopus ornatus* preserved in Bouin's solution from J. Arnold (University of Hawaii). The eggs were in an early stage of development and measured 3.2–3.3 mm in length and about 1.05 mm in width.

Octopus cyanea

(Figures 1C, E, F, 3)

Material examined: 56 specimens: 1.1–2.3 mm ML. Voucher SBMNH 35116 (7 specimens).

Body proportions: Mantle Length: 1.1–2.0 mm; Head Width: 1.0–1.6 mm (0.74–*0.82*–0.95); Eye Diameter: 0.3–0.5 mm (0.23–*0.28*–0.33); Arm Length: 0.48–0.80 mm (0.37–*0.42*–0.48); Arm Length Formula: subequal.

Suckers: Number per arm: 3; Largest diameter: 0.12–0.4 mm (0.07–*0.1*–0.12); Smallest diameter: 0.10–0.14 mm (0.07–*0.08*–0.10); Sucker Diameter Formula: $1 = 2 > 3$.

Tegumental chromatophores: Dorsal Arms: two series, 3 or 4 pairs; Ventral Arms: two series, 2–4 pairs; Arm Base: 6; Funnel: 2+2, rarely 3+2; Dorsal Mantle, Anterior Margin: simple band, 2 or 3; Posterior Region: 4–6; Ventral Mantle, Anterior Margin: 5, occasionally 4; Midregion: 6 across, occasionally 4, 5, or 7; Supravisceral: 8–10.

Extrategumental chromatophores: Dorsal Head: 4+4+2; Dorsal Eye: 2/eye; Ventral Head: 2.

Remarks: The unusual number of arm base chromatophores (6), while difficult to count, is an important systematic character. Chromatophores of the ventral arms are more vivid than those of the dorsal arms. Chromatophores of the Dorsal Mantle, Anterior Margin are difficult to see and among the first to fade in preservation. Occasionally a few small tegumental chromatophores are present on the head between the eyelids and arms. Stage I terminates between 1.6 and 1.8 mm ML.

Type A

(Figure 3)

Material examined: 11 specimens: 1.2–2.3 mm ML. Voucher SBMNH 35117 (5 specimens).

Body proportions: Mantle Length: 1.2–1.6 mm; Head Width: 1.05–1.25 mm (0.75–*0.82*–0.92); Eye Diameter: 0.30–0.35 mm (0.21–*0.24*–0.29); Arm Length: 0.50–0.72 mm (0.37–*0.44*–0.51); Arm Length Formula: subequal.

Suckers: Number per arm: 3; Largest diameter: 0.10–0.12 mm (0.07–*0.08*–0.08); Smallest diameter: 0.08–0.09 mm (0.06–*0.06*–0.07); Sucker Diameter Formula: 1 = 2 > 3.

Tegumental chromatophores: Dorsal Arms: two series, 4 or 5 pairs; Ventral Arms: two series, 4 or 5 pairs; Arm Base: 8; Funnel: typically 3+2, other patterns include 3+1, 4+1, 3+2, 4, 2+2; Dorsal Mantle, Anterior Margin: 3 or 4 across in simple band; Dorsal Mantle, Posterior Tip: 20–25; Ventral Mantle, Anterior Margin: 0; Ventral Mantle, Midregion: 12–15 across; Supravisceral: 11–15.

Extrategumental chromatophores: Dorsal Head: 2+4+4; Dorsal Eye: 3, occasionally 4; Ventral Head: 2.

Remarks: Dorsal Head chromatophores are especially vivid. Funnel chromatophores are minute and mostly concentrated at the orifice. The anterior region of the ventral mantle is bare or has only a few chromatophores. The mantle chromatophores are very small and extend over the Posterior Region of the mantle. A few small superficial chromatophores are found over the anterior eye region. Stage I terminates between 1.7 and 1.8 mm ML.

Type B

(Figure 3)

Material examined: 18 specimens: 1.1–2.2 mm ML. Voucher SBMNH 35118 (6 specimens).

Body proportions: Mantle Length: 1.25–1.55 mm; Head Width: 1.20–1.45 mm (0.86–*0.93*–0.97); Eye Diameter: 0.35–0.45 mm (0.28–*0.30*–0.31); Arm Length: 0.62–0.92 mm (0.48–*0.56*–0.62); Arm Length Formula: subequal.

Suckers: Number per arm: 3; Largest diameter: 0.12–0.14 mm (0.08–*0.09*–0.10); Smallest diameter: 0.10 mm (0.06–*0.07*–0.08); Sucker Diameter Formula: 1 ≥ 2 > 3.

Tegumental chromatophores: Dorsal Arms: two series, 3–5 pairs; Ventral Arms: two series, 3 or 4 pairs; Arm Base: 8; Funnel: 2+2+2, 1+2+2 or 2+1+2, occasionally 2+2 or 2+3; Dorsal Mantle, Anterior Margin: 4–6 across in simple band, occasionally 3; Dorsal Mantle, Posterior Region: few; Ventral Mantle, Anterior Margin: 2–6 across; Ventral Mantle, Midregion: 9–12 across; Supravisceral: 8–17.

Extrategumental chromatophores: Dorsal Head: 2+4+4; Dorsal Eye: 3, occasionally 4; Ventral Head: 2.

Remarks: This species is most easily confused with Type A but can be separated by the arrangement of chromatophores on the Funnel and Ventral Mantle fields and by the larger size of the Ventral Mantle chromatophores. In addition, in this species the Posterior Region of the mantle is generally bare or contains only a few, scattered, large chromatophores. In Type A the Posterior Region is covered with numerous small chromatophores.

Dorsal Head chromatophores are especially large and vivid. Funnel chromatophores are all large and none are on the orifice. A few small superficial chromatophores may be present over the anterior eye region. Stage I terminates at 1.6 mm ML.

Type C

(Figure 3)

Material examined: 40 specimens: 1.0–3.6 mm ML. Voucher SBMNH 35119 (6 specimens).

Body proportions: Mantle Length: 1.3–1.5 mm; Head Width: 0.95–1.3 mm (0.70–*0.82*–0.88); Eye Diameter: 0.35–0.50 mm (0.25–*0.31*–0.38); Arm Length: 0.54–0.70 mm (0.40–*0.45*–0.54); Arm Length Formula: 3 > 2 > 1 > 4.

Suckers: Number per arm: 3; Largest diameter: 0.12–0.14 mm (0.08–*0.10*–0.11); Smallest diameter: 0.08–0.10 mm (0.06–*0.06*–0.08); Sucker Diameter Formula: 1 > 2 > 3.

Tegumental chromatophores: Dorsal Arms: 0 in youngest; Ventral Arms: variable; Arm Base: 4, all ventral; Funnel: 2, occasionally 3; Ventral Mantle, Midregion: 2–4 across in simple band; Supravisceral: 6 or 7.

Extrategumental chromatophores: Dorsal Head: 2+4+2, occasionally 4+2; Dorsal Eye: 1, occasionally 2; Ventral Head: 0, occasionally 2.

Remarks: The few, characteristic Ventral Mantle chromatophores frequently were difficult to detect. The diagnostic larger size of arm III was also difficult to detect in the smallest specimens. This arm becomes progressively longer in larger specimens. Ventral Arm chromatophores are usually difficult to see or are absent in the youngest specimens. Sometimes a small chromatophore can be found on each side of each ventral arm indicating a future double series. This feature may be more easily seen on arm III although this arm often has an additional single proximal chromatophore in the midline. If only the latter is detected one could mistakenly conclude that the arm will develop a single series of chromatophores. The youngest specimens can be confused with Type D when the arm length or ventral chromatophore patterns prove difficult to distinguish. However, in these cases, the patterns of Dorsal Head chromatophores can separate these species. Occasionally in Type C paralarvae the anterior set of Dorsal Head chromatophores is missing. The chromatophore count then becomes 4+2 which can be confused with the 2+2+2 count of Type D. Type D, however, never has the first two series fully aligned into a simple band. Stage I of Type C terminates at 1.4–1.5 mm ML. The large arm III develops buds first. Other arms develop buds between 1.6 and 1.8 mm ML. This type of paralarva is commonly referred to as a "macrotritopus."

Type D

(Figure 3)

Material examined: 57 specimens: 1.0–4.0 mm ML. Voucher SBMNH 35120 (11 specimens).

Body proportions: Mantle Length: 1.0–2.0; Head Width: 0.65–1.40 mm (0.65–*0.81*–1.27); Eye Diameter: 0.22–0.50 mm (0.21–*0.25*–0.29); Arm Length: 0.32–0.68 mm (0.31–*0.34*–0.37); Arm Length Formula: subequal.

Suckers: Number per arm: 3; Largest diameter: 0.08–0.12 mm (0.06–*0.07*–0.07); Smallest diameter: 0.06–0.12 mm (0.05–*0.06*–0.07); Sucker Diameter Formula: 1 = 2 ≥ 3.

Tegumental chromatophores: Dorsal Arms: one series, number increases with size; Ventral Arms: one series, number increases with size; Arm Base: 4; Funnel: 2, occasionally 1; Ventral Mantle, Posterior Region: 2; Supravisceral: 5–9.

Extrategumental chromatophores: Dorsal Head: 2+2+2; Dorsal Eye: 1; Ventral Head: 0.

Remarks: Chromatophores are large but generally faint. The Arm Base chromatophores are located at the juncture of arms I and II and at the juncture of arms III and IV. All arms have a single chromatophore proximally in the aboral midline in the smallest specimens, although these may be difficult to see. This becomes a diagnostic single series on each arm in older paralarvae. The diagnostic pair of Ventral Mantle, Posterior Region chromatophores is often difficult to see, as well. This species is most easily confused with young Type C paralarvae. (See **Remarks** under that species). Stage I terminates at 2.0 mm ML.

Type E

(Figures 1A, B, 4)

Material examined: 17 specimens: 1.4–2.9 mm ML. Voucher SBMNH 35121 (6 specimens).

Body proportions: Mantle Length: 1.4–2.1 mm; Head Width: 1.05–1.25 mm (0.56–*0.71*–1.00); Eye Diameter: 0.35–0.45 mm (0.21–*0.27*–0.33); Arm Length: 0.56–0.92 mm (0.35–*0.46*–0.57); Arm Length Formula: subequal.

Suckers: Number per arm: 4; Largest diameter: 0.14–0.18 mm (0.08–*0.10*–0.12); Smallest diameter: 0.10–0.12 mm (0.06–*0.07*–0.08); Sucker Diameter Formula: 2 > 1 = 3 > 4 or 2 ≥ 3 ≥ 1 ≥ 4.

Tegumental chromatophores: Dorsal Arms: two series, 4 or 5 pairs; Ventral Arms: two series, 3 pairs; Arm Base: 8; Funnel: 2+2+2, occasionally 1+2+2 or 3+2+2; Dorsal Mantle, Anterior Margin: 3 or 4 across in simple band; Dorsal Mantle, Posterior Region: 8–20; Ventral Mantle, Anterior Margin: 4–7; Ventral Mantle, Midregion: 5–7 across; Supravisceral: approximately 20–30.

Extrategumental chromatophores: Dorsal Head: 2+4+4, occasionally 2+3+4 or 3+4+4 or up to 15 arranged irregularly; Dorsal Eye: 3–5; Ventral Head: 2.

Remarks: The mantle is distinctly elongate; this feature combined with the large number of supravisceral chromatophores is diagnostic for Type E species. The chromatophores on the ventral mantle form a broad complex stripe. The basic 2+4+4 Dorsal Head chromatophore pattern is often obscured as size increases by additional Dorsal Head chromatophores. A few small superficial chromatophores may be present over the anterior eye region. Stage I terminates between 2.0 and 2.5 mm ML.

Preserved eggs and hatchlings with color photographs were obtained from B. Houck, presently at the University of Portland, Oregon. These allowed positive identification with adults commonly known as the "crescent octopus." Eggs are about 3 mm in length (Houck, 1977).

Type F

(Figure 4)

Material examined: 6 specimens: 1.1–2.0 mm ML. Voucher SBMNH 35122 (3 specimens).

Body proportions: Mantle Length: 1.1–1.6 mm; Head Width: 0.9–1.2 mm (0.67–*0.72*–0.76); Eye Diameter: 0.34–0.45 mm (0.23–*0.27*–0.32); Arm Length: 0.45–0.85 mm (0.35–*0.41*–0.52); Arm Length Formula: subequal.

Suckers: Number per arm: 4; Largest diameter: 0.10–0.13 mm (0.07–*0.08*–0.09); Sucker Diameter Formula: 1 = 2 = 3 ≥ 4.

Remarks: Generally no chromatophores can be detected. One specimen (1.6 mm ML), however, had some faint chromatophores in the following pattern: one at the base of each arm I, two in one series on each arm III, and three in one series on each arm IV. Dorsal Head chromatophores were 2+2 and one chromatophore lay over each eye. About 8–10 supravisceral chromatophores were present. Köllikers organs are numerous. Stage I terminates between 1.6 and 2.0 mm ML.

Type G

(Figure 4)

Material examined: 3 specimens: 1.3–2.3 mm ML. Voucher SBMNH 35125 (1 specimen).

Body proportions: Mantle Length: 1.3–2.3 mm; Head Width: 1.2–1.6 mm (0.71–*0.81*–0.88); Eye Diameter: 0.35–0.55 mm (0.24–*0.26*–0.27); Arm Length: 0.70–1.10 mm (0.33–*0.46*–0.57); Arm Length Formula: subequal.

Suckers: Number per arm: 4; Largest diameter: 0.19 (2.3 mm ML specimen); Smallest diameter: 0.12 (2.3 mm ML specimen); Sucker Diameter Formula: 1 = 2 = 3 ≥ 4 or 2 = 3 > 1 > 4.

Tegumental chromatophores: Dorsal Arms: irregular between one and two series; Ventral Arms: irregular between one and two series; Arm Base: uncertain; Funnel: 0; Dorsal Mantle, Anterior Margin: 0; Dorsal Mantle, Anterior Region: 7–9 across in a complex band that is continuous with the Ventral Mantle, Anterior Region; Ventral Mantle, Anterior Region: 7–13 across in wide complex band; Supravisceral: 6–8 (not shown in Figure 4).

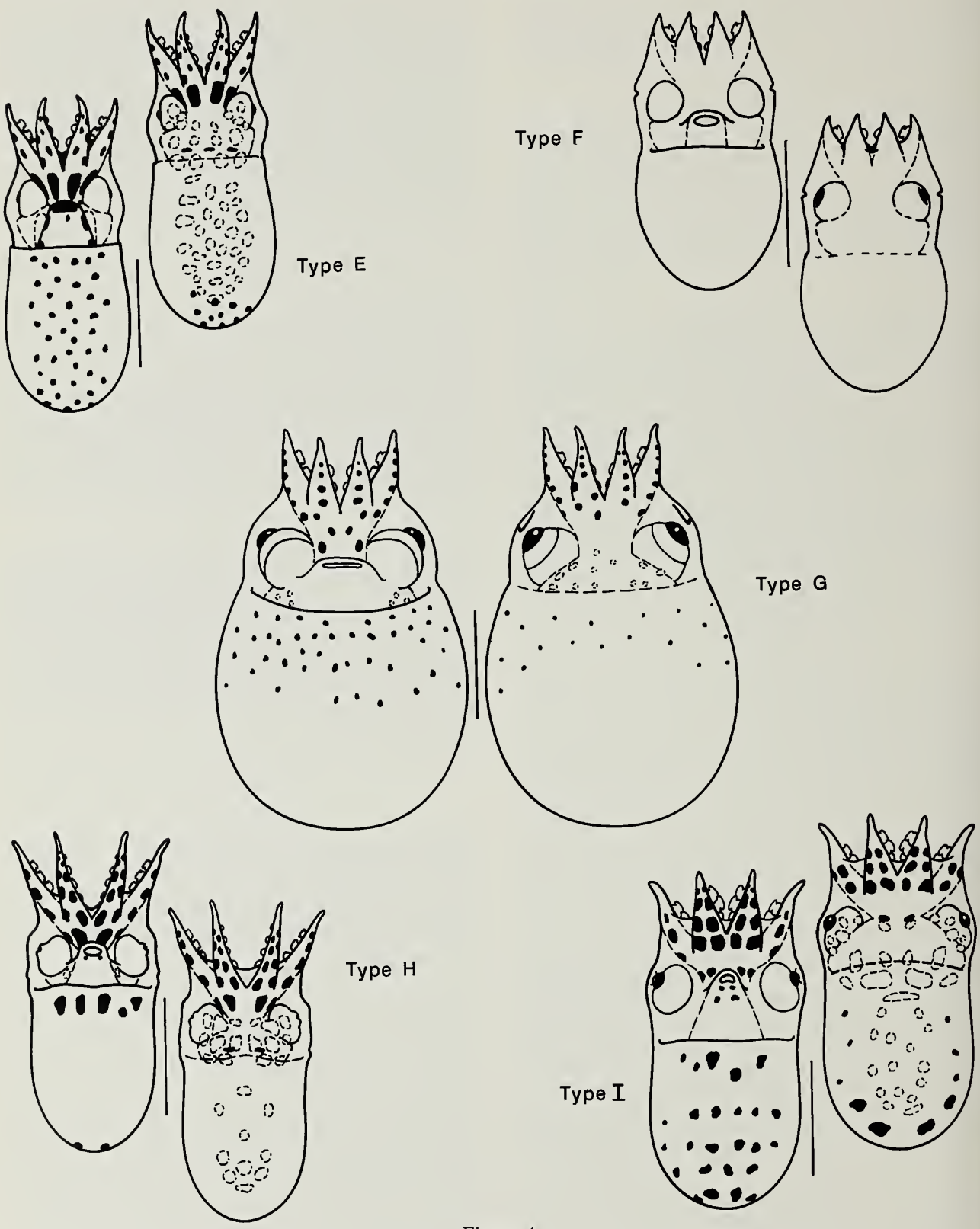


Figure 4

Dorsal and ventral views of Stage I octopodid paralarvae with four suckers per arm. Scale bar = 1 mm.

Extrategumental chromatophores: Dorsal Head: about 12 in irregular arrangement; Dorsal Eye: uncertain; Ventral Head: about 8, scattered.

Remarks: Some chromatophores had faded by the time they were counted, resulting in low or zero counts in some cases. When all chromatophores are faded, this species is virtually inseparable from Type D paralarvae. Both are squat and rather gelatinous. The size at which Stage I terminates is unknown.

Type H

(Figure 4)

Material examined: 43 specimens: 1.0–4.0 mm ML. Voucher SBMNH 35123 (11 specimens).

Body proportions: Mantle Length: 1.0–2.0 mm; Head Width: 1.00–1.50 mm (0.75–*0.85*–1.00); Eye Diameter: 0.25–0.40 mm (0.20–*0.24*–0.29); Arm Length: 0.24–0.36 mm (0.18–*0.20*–0.24); Arm Length Formula: subequal.

Suckers: Number per arm: 4; Largest diameter: 0.08–0.12 mm (0.05–*0.08*–0.09); Smallest diameter: 0.04–0.08 mm (0.03–*0.04*–0.06); Sucker Diameter Formula: 2 > 1 = 3 > 4.

Tegumental chromatophores: Dorsal Arms: two series, 4 pairs; Ventral Arms: two series, 4 pairs; Arm Base: 8; Funnel: 2+2, occasionally 2; Dorsal Mantle, Anterior Margin: 2–4 across in simple band; Ventral Mantle, Anterior Margin: 5 or 6, occasionally 7 across in simple band; Ventral Mantle, Posterior Region: 2 or 3; Supravisceral: 12–17.

Extrategumental chromatophores: Dorsal Head: 2+4+4; Dorsal Eye: 3; Ventral Head: 2.

Remarks: All chromatophores are large and vivid. Eye chromatophores are difficult to see against the dark eyes. Distal Funnel chromatophores are very small and lie near the orifice. Posterior Funnel chromatophores, when present, are only slightly larger and lie near the others. One or two small superficial chromatophores are often present anterior to the eye opening. The Ventral Mantle, Anterior Margin chromatophores are diagnostic. Stage I terminates between 2.0 and 4.0 mm ML.

Type I

(Figure 4)

Material examined: 22 specimens: 1.1–2.2 mm ML. Voucher SBMNH 35124 (6 specimens).

Body proportions: Mantle Length: 1.1–2.0 mm; Head Width: 1.05–1.25 mm (0.55–*0.79*–1.05); Eye Diameter: 0.35–0.45 mm (0.20–*0.27*–0.35); Arm Length: 0.62–0.74 mm (0.39–*0.51*–0.68); Arm Length Formula: subequal.

Suckers: Number per arm: 4; Largest diameter: 0.16–0.23 mm (0.11–*0.14*–0.17); Smallest diameter: 0.10–0.12 mm (0.06–*0.08*–0.10); Sucker Diameter Formula: 2 > 3 > 4 > 1.

Tegumental chromatophores: Dorsal Arms: two series, 2 or 3 pairs; Ventral Arms: two series, 3 or 4 pairs; Arm Base: 8; Funnel: 2+2, occasionally 2; Dorsal Mantle, Anterior Margin: 0; Dorsal Mantle, Posterior Region: 4–6; Ventral Mantle, Anterior Margin: 3–6; Midregion: 4–6 across; Supravisceral: 12–17.

Extrategumental chromatophores: Dorsal Head: 2+4+4; Dorsal Eye: 3–5; Ventral Head: 0.

Remarks: The small size of sucker No. 1 (proximal sucker) and the large size of sucker No. 2 are diagnostic of Type F paralarvae in Hawaiian waters. Chromatophores are large and vivid, especially so in the fields on the dorsal surfaces. Anterior Funnel chromatophores are very small and located on the funnel orifice. Scattered chromatophores may extend from the Dorsal Mantle, Posterior Region along the dorsolateral margins of the mantle. The number of Dorsal Eye chromatophores increases with size. Stage I terminates between 2.0 and 2.3 mm ML.

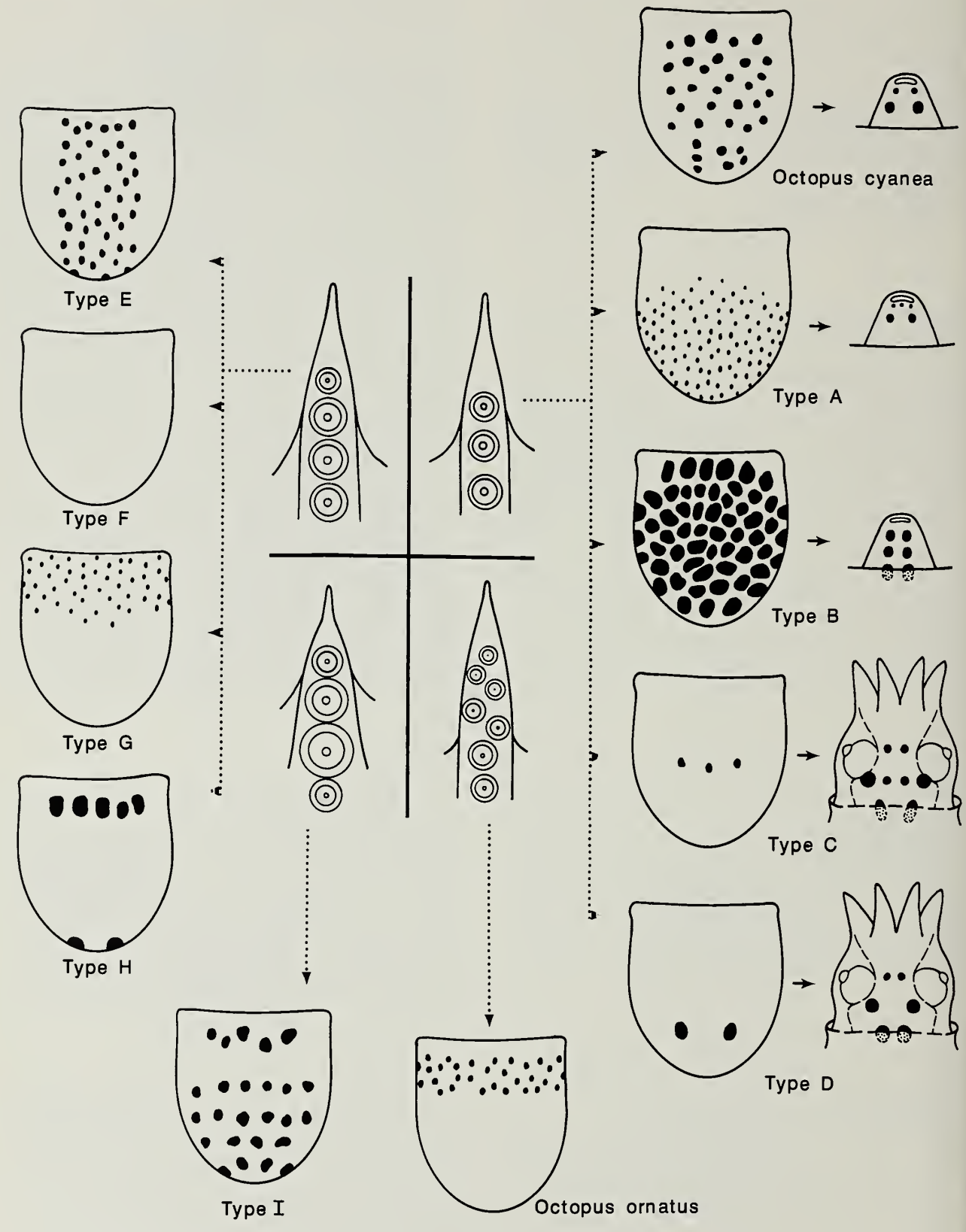
Eggs and their hatchlings were available from J. Arnold who obtained them from W. Van Heukelem. Although labelled as *Scaeurgus*, they probably came from an undescribed species with certain similarities to *Scaeurgus* (Van Heukelem, personal communication). The material, preserved in Bouin's fluid, measured 3.0 mm for eggs near hatching and 1.2–1.3 mm ML for hatchlings. Our smallest specimens taken from the plankton are smaller than this, but this is not surprising considering the variability in size measurements due to state of contraction following fixation.

Older Stages

Our collection of paralarvae between Stage I and settling (metamorphosis) is incomplete. Since little is known for most octopodids regarding the size they can reach while planktonic, the largest identifiable paralarvae that we have in our collections are listed here. These data do not imply size at metamorphosis. *Octopus ornatus*, 7.3 mm ML; *O. cyanea*, 11.0 mm ML; Type A, 6.1 mm ML; Type B, 6.0 mm ML; Type C, 13.5 mm ML; Type D, 6.5 mm ML; Type E, 15.0 mm ML (tentative identification); Type F, 5.5 mm ML; Type G, 5.8 mm ML; Type H, 6.1 mm ML; Type I, 7.7 mm ML.

Other Species

Two additional types of octopodid paralarvae are known to occur in Hawaiian waters but have not been described here. W. Ikehara (Hawaii Division of Aquatic Resources) reported finding a small brooding octopus in intertidal waters on Oahu. He removed the egg string and reared the embryos through hatching. Photographs that he took reveal a paralarva with very different chromatophore patterns from any described here. The arms had chromatophores in 2 rows; the ventral mantle was covered with


Octopus cyanea
Type E
Type A
Type F
Type B
Type G
Type C
Type H
Type D
Type I
Octopus ornatus

numerous small, densely packed chromatophores; the dorsal mantle had many small but more scattered chromatophores; about 50 supravisceral chromatophores appeared to be present. The identity of the adult is unknown, but fishermen report that it is fairly common in the intertidal zone throughout Hawaii.

The other undescribed paralarva was taken in a plankton tow and is very similar to Type F, but was more gelatinous and had a slightly more restricted mantle opening as well as many, very tiny, faint chromatophores on the head, funnel, and mantle. Our single specimen was just beyond Stage I and most chromatophores had faded before we were able to record the patterns.

Integumental Pores

We examined some paralarvae with the scanning electron microscope in order to photograph the sucker arrangement and to demonstrate the distinctive appearance of sucker buds that mark the end of Stage I (Figures 1A–D). This examination enabled us to examine other features as well. (1) We expected to find sensory organs on the peculiar attenuate arm tips, but did not. The function of these elongate, bare arm tips is unknown. (2) We observed large numbers of pores covering the arms, head, and mantle. In many areas the pore apertures constitute over 10% of the body surface (Figure 1E). High magnification of the pores reveals small spheres in the apertures (Figure 1F). We assume that the pores are the openings of mucus-secreting organs and the spheres are the secretory products before expansion in water. The high pore density was apparent only on paralarvae hatched in the laboratory. We searched the surfaces of several types of net-caught paralarvae of various sizes and, while some pores could be found, densities were always low.

DISCUSSION

We believe that all the paralarval types described here represent valid species. All are characterized by a suite of consistent characters. Further, we are confident that they represent Hawaiian species. Although the duration of Stage I is unknown for most species, it is probably very short. For example, sucker buds appear on the arms of three-day-old hatchlings of *Octopus bimaculatus* (AMBROSE, 1981).

Nearly all Stage I paralarvae of the Hawaiian octopodid species can be recognized easily by their chromatophore patterns. Virtually every field of chromatophores exhibited specific characteristics in some species. The Ventral Mantle field, however, showed the greatest range of chromatophore patterns and was the most useful for identification. Both the pattern and the number of chromatophores (within a specific chromatophore field) were usually distinctive. Pattern changes beyond Stage I paralarvae were not presented in this study but did vary between species. For example, in Type D, except for increases in chromatophore numbers on the longer arms, the pattern remained unchanged up to at least 6 mm ML, while in Type B increases in numbers of chromatophores, especially in Dorsal Mantle chromatophores, began by 2–3 mm ML.

The number of suckers per arm in Stage I paralarvae also proved to be a valuable feature for identification. Of the 11 species where Stage I paralarvae were examined, five species had three suckers per arm, five species had four suckers, and one species had seven suckers. This character is unambiguous, easily detected, and because it separates major suites of species, it is extremely useful for identification. Sucker size was diagnostic in one species (Type I). In the younger stages, only one species (Type C: "macrotritopus") had a distinctive arm formula.

These characters are suitable for constructing a key based on icons. Such a key (Figure 5) is far simpler and faster to use than a typical dichotomous key. One simply follows the arrows from the original choice of four drawings. Secondary characters are indicated by non-branching arrows.

The distribution of Kölliker's organs provided another potentially valuable systematic character. The high density of these bristlelike structures, especially on the ventral surfaces of the head, was characteristic of several species (*e.g.*, Types E and F). However, intraspecific variations were considerable and detection of the organs proved to be difficult. Thus, we made no attempt to quantify this character, and we used it only as a guide when chromatophore patterns had faded.

The paralarvae of only three types, *Octopus cyanea* and Types E and I, can be connected to adults with certainty (adults of the latter two species are undescribed). In these cases, hatchlings were obtained and examined from known females that spawned in captivity. The only other method of positive identification requires the rearing of advanced paralarvae taken from plankton. We reared Type H for three months and Type D for about six months. Although growth of Type H was minimal during this period, the octopus metamorphosed into its benthic form and displayed distinctive chromatophore patterns and unusual sculpturing. It clearly does not belong to any known Hawaiian species. Type D grew better than Type H in captivity but remained small and nondistinct. It, also, cannot be related to any known species. In regions like Hawaii where adult octopods of many species are scarce and cryptic, rearing

←

Figure 5

Key to Hawaiian octopodid paralarvae. Begin by picking the appropriate drawing from the central four, then follow dotted lines and arrows. On the right, secondary characters are shown for species with three arm suckers. Funnel chromatophore patterns must be used with caution due to intraspecific variability (see text).

paralarvae captured in the plankton may ultimately prove to be the more useful technique for paralarval identification.

Distinctive paralarval features suggest adult affinities for a few additional species:

(1) We are confident of the identification of paralarvae of *Octopus ornatus* owing to their similarity to the paralarva of *O. macropus* illustrated by NAEF (1928). The Hawaiian member of the *O. macropus* species complex is *O. ornatus*. Not only do the Hawaiian paralarvae have similar chromatophore patterns, but they also share the same unusual number (7) of Stage I arm suckers.

(2) In the Atlantic, "macrotritopus" paralarvae have been shown to be young of *Octopus defilippi* (HANLON *et al.*, 1980; NESIS & NIKITINA, 1981; HANLON *et al.*, 1985). Although this species is not known to occur in Hawaiian waters, it or a sibling species must be present since our paralarvae (with the exception of differences in chromatophore patterns) are very similar to the macrotritopus previously described. We, therefore, refer specimens of Type C to the *O. "defilippi"* species complex.

(3) BOLETZKY (1977, 1984) described the paralarvae of *Scaeurgus unicirrus* from the Mediterranean and we have examined some of his specimens. The paralarvae of Type F are very similar to these. Unfortunately, the chromatophores of Type F are usually absent (in contrast to the Mediterranean paralarvae). Nevertheless, in one advanced Stage I paralarva some faint chromatophores were present. This paralarva seemed to have a single row of chromatophores on the arms as is characteristic of Mediterranean paralarvae. This is an unusual feature in Hawaiian paralarvae. In addition, both Hawaiian and Mediterranean paralarvae have four suckers in Stage I and high concentrations of Kölliker's organs. We tentatively assign Type F to *Scaeurgus patagiatus*.

The similarity of the paralarvae of *Octopus ornatus* and Type C to their Atlantic siblings suggests that paralarval morphology and chromatophore patterns are conservative and that these characters may be useful in octopodid systematics above the species level.

Our SEM observations of densely packed secretory pores on hatchlings, but not larger paralarvae, are puzzling. Perhaps the secretion of mucus is important either during the late embryonic stages or for a short period after hatching. We suggest that mucous secretions in the latter case might form a "drogue" that would assist the young octopus in remaining near the surface while currents transport it offshore. Hatchlings observed in the laboratory were strongly negatively buoyant and had to swim vigorously to remain near the surface of their container. Mucous secretions have not been observed in laboratory-reared hatchlings, perhaps because water turbulence or aquarium walls destroy any mucous structures. A mucous drogue would require far less energy expenditure than swimming and the motionless, drifting paralarvae might be less conspicuous to predators.

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The Pelagic Octopus *Tremoctopus violaceus* Delle Chiaje, 1830, from Southern Australian Waters

by

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Abstract. The octopod genus *Tremoctopus* has been recorded previously from eastern Australian waters by C. C. Lu and J. U. Phillips in 1985. Locality details of these specimens are given here for the first time, and new records of specimens from Western Australia and South Australia are recorded. The two adult females from South Australia extend the range of *T. violaceus* to latitude 36°S and indicate that the Leeuwin Current, with water of tropical origin from the western Australian coast, may have a more easterly influence than previously thought.

INTRODUCTION

Octopods generally are regarded as benthic animals. However, a number of species including those of *Tremoctopus* are pelagic and have widespread distributions. *Tremoctopus* is easily distinguished by its somewhat squidlike appearance and possession of two pairs of conspicuous pores in the web at the base of the arms: one pair dorsally and another pair ventrally, adjacent to the funnel (Figure 1). The genus was revised in detail by THOMAS (1977), but no specimens were recorded from Australian waters. The first published record of *Tremoctopus* from Australia appears to be that of LU & PHILLIPS (1985) who recorded *T. violaceus* Delle Chiaje, 1830, from the eastern Australian coast ("New South Wales," p. 34) but gave no details of specimens or localities. The present paper provides details about these and other specimens. Two adult females are the first adults obtained from southern Australia and provide a substantial range extension for this broadly distributed species.

DELL (1952) recorded *Tremoctopus violaceus* from New Zealand, so its occurrence in eastern Australian waters is not surprising (ALLAN, 1945); however, the occurrence of this circumtropical species in southern Australian waters requires explanation.

MATERIAL EXAMINED

Details of Australian specimens deposited in various Australian museums follow; body measurements (Table 1) are according to ROPER & VOSS (1983) and beak dimensions (Table 2) follow those devised by WOLFF (1984).

Australian Museum, Sydney (AM)

(1) Adult female (AM C156235), 320 mm ML, without data.
(2) Adult female (AM C516), 255 mm ML, Manly, Sydney, New South Wales, presented by H. Prince, 1894.

Museum of Victoria, Melbourne (NMV)

(1) Juvenile (male?) (NMV F53416), 7.0 mm ML, approx. 160 km NE of Cairns, Queensland (15°57'S, 146°52'E), trawled in 0–850 m by RV *Lady Basten*, 5 December 1981.
(2) Juvenile (male?) (NMV F53417), 11.1 mm ML, approx. 300 km E of Swansea, New South Wales (33°12'S, 154°52'E), trawled in 0–200 m by RV *Sprightly*, 22 August 1982.
(3) Juvenile (male?) (NMV F53414), 5.4 mm ML, approx. 350 km E of Wollongong, New South Wales (34°29.5'S, 154°42.1'E), trawled in 20 m by RV *Soela*, 30 September 1981.
(4) Juvenile (male?) (NMV F53415), 30.0 mm ML, approx. 355 km E of Batemans Bay, New South Wales (35°34.6'S, 154°13'E), trawled in 20 m by RV *Soela*, 4 October 1981.

Western Australian Museum, Perth (WAM)

(1) Adult female (WAM 964.87), 265 mm ML, stranded on Shelly Beach, Albany, Western Australia, collected by J. Combe, April 1986. (Damaged).
(2) Adult female (WAM 965.87), approx. 230 mm ML,

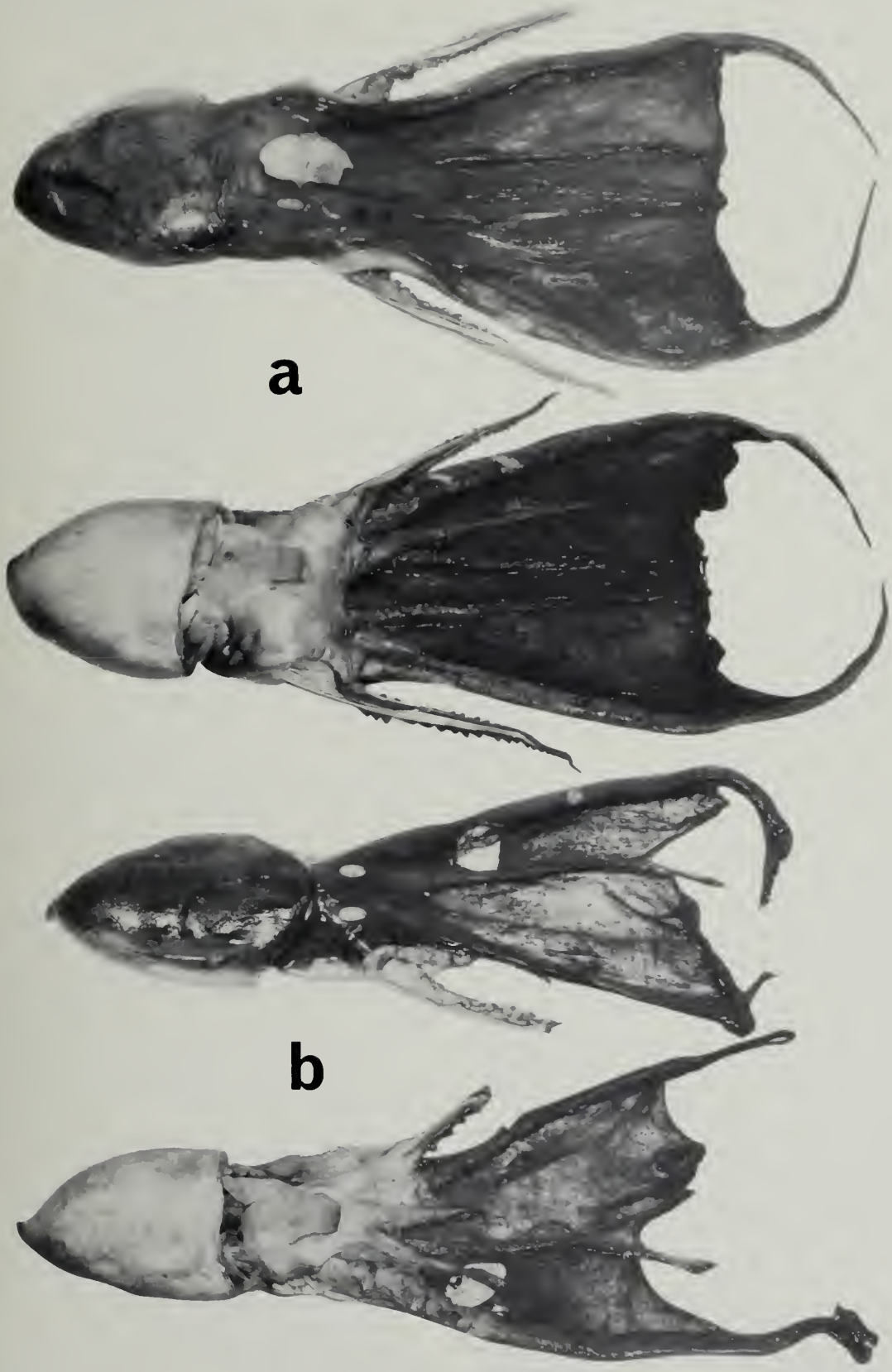

Figure 1

Tremoctopus violaceus adult females from South Australia. a, 230 mm ML, Outer Harbour (SAM D17601); b, 230 mm ML, D'Estrees Bay, Kangaroo Island (SAM D17602).

Table 1

Tremoctopus violaceus; body measurements of South Australian specimens from Outer Harbour (SAM D17601) and Kangaroo Island (SAM D17602).

Character	SAM D17601	SAM D17602
Weight (fresh)	2.75 kg	1.05 kg
Gill number	14	14
Measurement (mm)		
Total length	940	720
Mantle length (dorsal)	230	230
Mantle length (ventral)	175	180
Mantle width (maximum)	175	130
Head length	35	30
Head width	140	80
Arm length I (left/right)	410/460 (both tips missing)	330/290
Arm length II (left/right)	710/720	missing/480
Arm length III (left/right)	350/350	200 (incomplete)/missing
Arm length IV (left/right)	345/½ missing	140/150 (both incomplete)
Arm width index	23/230 (10%)	28/230 (12.2%)
Web depth A	to arm tips	to arm tips
Web depth B	to arm tips	to arm tips
Web depth C	100	damaged
Web depth D	105	110
Web depth E	60	75
Funnel length (ventral)	82	80
Free funnel length	40	45
Funnel width (at opening)	26	24
Pallial aperture	140	90
Eye diameter	18	10
Pore size, ventral (left/right)	12 × 16/10 × 17	12 × 19/12 × 17
Pore size, dorsal (left/right)	damaged/15 × 21	15 × 20/15 × 21

regurgitated by sperm whale or whale shark off Albany, Western Australia, donated by Cheyne Beach Whaling Co., 1975? (Partly decomposed).

(3) Juvenile (male?) (WAM 344.77), 4.5 mm ML, 73 km west of Rottnest Island, Western Australia, in surface net, collected by P. Cawthorn on FRV *Lancelin*, 7 October 1962.

South Australian Museum, Adelaide (SAM)

(1) Adult female (SAM D17601) (Figure 1a, Tables 1, 2), 230 mm ML, from midway between Section Bank and Saint Kilda, just north of Outer Harbour, South Australia (34°45′S, 138°30′E), alive in prawn trawl, collected by P. D. Vickers, 29 June 1984.

(2) Adult female (SAM D17602) (Figure 1b, Tables 1, 2), 230 mm ML, stranded on D'Estrees Bay Beach, Kangaroo Island, South Australia (35°44′S, 137°39′E), "recently dead," collected by V. F. H. Bell, 8 March 1986.

DISCUSSION

Two subspecies of *Tremoctopus violaceus* are currently recognised (THOMAS, 1977) but they are very similar morphologically. According to Thomas "the most striking difference between these two subspecies is the number of suckers on the hectocotylized arm of the males." In *T.*

Table 2

Tremoctopus violaceus; beak dimensions of South Australian specimens from Outer Harbour (SAM D17601) and Kangaroo Island (SAM D17602).

Character	Measurement (mm) SAM D17601	SAM D17602
Upper		
Hood length	17.2	15.0
Rostral length	12.0	9.8
Wing width	2.5	2.3
Rostral tip to inner margin of wing	13.2	10.0
Wing to crest length	24.5	21.9
Crest length	27.8	24.0
Jaw angle width	13.4	12.0
Lower		
Rostral tip to inner posterior corner of lateral wall	24.1	20.5
Rostral length	10.5	8.4
Rostral tip to inner margin of wing	20.9	17.6
Wing length	10.8	10.2
Jaw angle width	13.0	11.0

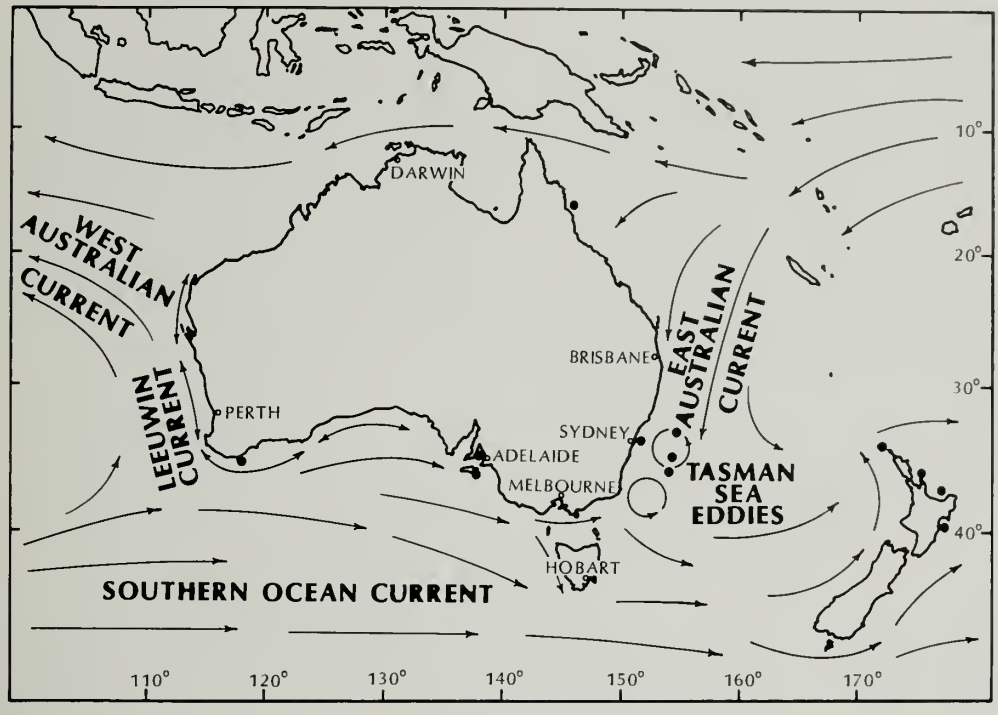

Figure 2

Major sea surface currents during winter (simplified) around New Zealand and Australia and records of *Tremoctopus* captures (●).

violaceus gracilis there are 19–22 pairs of transverse suckers on the distal portion of the arm and 27–29 pairs of suckers on the proximal portion, while *T. violaceus violaceus* has 15–19 and 22–23 pairs of suckers respectively. The females, however, are virtually identical, differing mainly in the mean number of gill filaments (13 for *T. v. violaceus* and 15 for *T. v. gracilis*) although both have the same range (13–16). Thus in the absence of males the subspecific identity of the Australian specimens cannot be confirmed, but based on the geographic distribution given for the two subspecies by THOMAS (1977) the Australian subspecies is most likely *T. v. gracilis* (Eydoux & Souleyet, 1852).

Tremoctopus violaceus is considered to be a circumtropical species (THOMAS, 1977) and even DELL's (1952) New Zealand records (Figure 2) are north of the subtropical convergence. The South Australian records thus represent a considerable range extension.

The occurrence of tropical species off New South Wales is not unexpected, as warm-core eddies are a common element of the East Australian Current and regularly carry pelagic cephalopods southward (BRANDT, 1983). However these eddies usually disintegrate before approaching Bass Strait (NILSSON & CRESSWELL, 1981) so they do not normally provide a vehicle for tropical species to reach South Australian waters. The most likely origin is from the west via the Leeuwin Current that carries water of tropical origin eastwards, predominantly in winter, and is considered responsible for the dispersal of other tropical marine species to southern Australia (MAXWELL & CRESSWELL, 1981).

The winter-time capture of the Outer Harbour specimen coincides with the presence of the Leeuwin Current. The specimen probably was attracted by the relatively warmer water of Gulf St Vincent and eventually was caught in shallow water (3–5 m) at the opening of Barkers Inlet, which carries thermally polluted water from Torrens Island Power Station. When captured it appeared to be in good condition but, judging by the digested remains of stomach contents, it had not fed recently. The specimen stranded on the southern side of Kangaroo Island probably was "lost" and could not survive the cooler waters of the Southern Ocean, *i.e.*, most likely it had been carried by the Leeuwin Current far enough southward that the temperatures had dropped below survival levels(?).

The South Australian records of *Tremoctopus* and also that of another tropical cephalopod, *Nautilus repertus* (=*N. pompilius*?) from Foul Bay, Investigator Strait (RIDDLE, 1920), indicate that the Leeuwin Current may, at times, have a more easterly influence than was previously thought.

The two South Australian specimens illustrate some interesting aspects of morphometry (Table 1). Although one specimen is more than twice the weight of the other, they both have the same mantle length. The larger specimen (SAM D17601), however, has a much greater mantle

and head width. THOMAS (1977) found that the relative width of the mantle decreases with an increase in size of small animals and later growth is isometric; also in adults, the mantle length continues to increase slightly faster than the head width. The larger South Australian specimen would thus appear to have rather wide body measurements for this species.

The stomach contents of all adult specimens were examined but were too decomposed or digested to be determined except for the South Australian specimens, which were much fresher, and the Western Australian specimen stranded on Shelly Beach. The stomach of the latter specimen (WAM 964.87) contained unidentifiable fish scales of at least two types (cycloid and ctenoid), cephalopod flesh (no beak!), and other remains. The specimen stranded on Kangaroo Island (SAM D17602) had only bits of green algae and the brown alga *Hormosira banksii* in the stomach, undoubtedly swallowed while being stranded. The stomach contents of the specimen caught near Outer Harbour (SAM D17601), however, consisted of polychaete jaws, spicules, and strands of tubular tissue that could be the intestinal lining of the same polychaete and several specimens of a trematode belonging to the Hemiuroidea. The polychaete jaws are identical to those of *Glycera americana* Leidy, 1855 (Glyceridae) which is a species that swarms around Outer Harbour in June–July coinciding with the capture of the octopus. The fact that the soft parts of the worms had been completely digested suggests that the octopus may have been in the vicinity of its capture for some time. The trematodes were immature(?) and could not be identified further; however, they belong to a group usually found in the digestive tract and stomach of marine fishes. THOMAS (1977) found that adult *Tremoctopus* fed chiefly on small fishes so this trematode could have been ingested via a fish host but there were no fish remains present and the trematodes were in good condition, suggesting that *Tremoctopus* might also be a host for these parasites.

The Western Australian specimens represent a new record for that state.

ACKNOWLEDGMENTS

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Morphological Variation in the Radula of *Placida dendritica* (Alder & Hancock, 1843) (Opisthobranchia: Ascoglossa/Sacoglossa) from Atlantic and Pacific Populations

by

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Abstract. *Placida dendritica* is a cosmopolitan, ascoglossan (=sacoglossan) species for which geographic variants have been difficult to define. However, examination of 54 radulae, 34 of these with an SEM, revealed a geographic pattern of Pacific Basin teeth with a cutting edge of regular truncate denticles, while North Atlantic and Mediterranean specimens had an edge of irregular, conical denticles. Body lengths ranged from 2 to 20 mm, ascending tooth row from 6 to 18 teeth, descending tooth row from 18 to 78, and total number of teeth for individuals from 28 to 93. Loose teeth in the ascus were recorded only in Australian and New Zealand samples. Highest tooth counts were from British Columbian specimens of 7 and 8 mm body length, and the next highest counts from 3 and 4 mm Australian and New Zealand specimens. Eleven contrasting collection sites are described, and the algal genus *Derbesia* is added to *P. dendritica* prey items.

INTRODUCTION

One of the consequences of geographic isolation, and a basic tenent in biology, is that genetic variants can more readily become established and thereby greatly hasten speciation. Over great distances, one easily assumes that there has been some degree of anatomical diversity and may even feel obligated to find it. Thus, it is not surprising that whenever a sea slug resembling the European sea slug *Placida* (*Hermaea*) *dendritica* (Alder & Hancock, 1843) was reported from a distant geographic region it was assumed to be a new species and confidently designated as such. At that time, the full spectrum of variation that can be encompassed by seasonal and individual variations was not appreciated. Thus, this animal has been known as *P. aoteana* Powell, 1937, in New Zealand, *P. babai* Marcus, 1982, in Japan, and *P. ornata* MacFarland, 1966, in California. The current taxonomic consensus (THOMPSON, 1973, 1976; GASCOIGNE, 1976; JENSEN, 1983; Marcus *in* BABA, 1986) is that a single species (*Placida dendritica*) ranges from Norway to the Mediterranean Sea; from Newfoundland to the Florida Keys and to Curaçao in the Lesser Antilles; from British Columbia to Mexico; and from Japan to eastern Australia and New Zealand.

That there are no reported differences in general anatomy nor in radular morphology between populations of this worldwide species is truly remarkable. Available literature implies that even its algal prey is consistent worldwide, the siphonalean Chlorophyta genus *Codium*. CLARK & FRANZ (1969) went so far as to state that it was highly unlikely that *Placida dendritica* could have existed in New England prior to a recent establishment of *Codium fragile* (Suringar) Hariot in that area. Recent examination of material in my collections, however, indicates that (1) *P. dendritica* does occur in areas devoid of *Codium*, and that (2) radular morphology does differ regionally.

MATERIALS AND METHODS

Specimens collected personally in New Zealand, Australia, Japan, British Columbia, Nova Scotia, and Newfoundland were also photographed alive with color transparencies. Additional preserved material was kindly supplied by the individuals indicated in Table 1, which lists localities, col-

Table 1

List of localities, collectors, dates, total numbers of specimens, and number of *Placida dendritica* radula examined by SEM.

Locality	Collector	Date	Total specimens	SEM
N.Z., Leigh	J. S. Bleakney	April 1981	54	2
N.Z., Otago Bay	J. S. Bleakney	11 May 1981	7	1
Aust., Botany Bay	J. S. Bleakney	17 Jan. 1981	42	4
Japan, Seto	J. S. Bleakney	1 Nov. 1980	3	1
Japan, Osaka Bay	I. Hamatani	18 Feb. 1961	6	3
B.C., Vancouver Isl.	J. S. Bleakney	Aug. 1980	4	1
B.C., Triangle Isl.	P. Lambert	21 Aug. 1974	2	2
B.C., Vancouver Isl.	G. Gibson	21 May 1988	18	3
N.S., Chester Basin	J. S. Bleakney	31 Aug. 1969	1	1
N.S., Bear River	J. S. Bleakney	26 July 1970	3	2
Newfd., Logy Bay	J. S. Bleakney	7 Aug. 1970	1	1
Ireland, Co. Donegal	B. E. Picton	29 May 1988	3	2
England, Loo	A. Kress	March 1970	20	4
Spain	J. Ortea	?	4	4
Italy, Naples	Panceri	1866	4	3
			172	34

lectors, dates, number of specimens available for this study, and the number of radulae examined by SEM.

Radulae from each locality were prepared for SEM examination by the tissue solubilizer method of BLEAKNEY (1982) and 148 SEMs taken. The tiny penial style proved difficult to prepare for SEM, but several samples proved adequate for verification of structures suspected from light microscopy observation. Standard microscope slide mounts of radulae and penial styles were photographed, and additionally many of the radulae were photographed through a microscope during and/or at the end of the tissue solubilizer treatment. Overall, 130 black and white photographs were taken.

RESULTS AND DISCUSSION

Diversity of Algal Food

The morphology of *Placida dendritica* teeth can be altered by feeding on algae. The tooth tip can be blunted and the cutting edge worn down (Figure 20) and in some cases even chipped and broken (Figures 1, 2, 5).

Although *Codium* is the reported main food of *Placida dendritica* (JENSEN, 1980), *Bryopsis* was mentioned by MILLEN (1980) for British Columbia and by THOMPSON (1976) for Europe. However, in Newfoundland and Nova Scotia where *Codium* is absent and *Bryopsis* is very rare, I found this ascoglossan feeding and spawning upon *Derbesia marina* (Lymgbye) Sal. This genus is also a member of the Siphonales, an algal group with coenocytic filaments much preferred by algal sapsuckers. This small alga is easily overlooked, as it usually occurs as a small tuft, mat, or coating on the surface of larger algae or upon animal exoskeletons. Interestingly, specimens of *P. dendritica* collected at Seto, Japan, were on *Derbesia lamourouxii* (J. Agardh) Solier (=*marina*?) in a region where this ascoglossan has been reported to feed only upon *Codium* (BABA, 1955, 1986). At the Leigh Marine Laboratory, New Zealand, *P. aoteana* was collected from both *Codium adhaerens*

→

Explanation of Figures 1 to 7

Figure 1. Portion of radular ribbon with attached teeth from 20-mm long *Placida dendritica,* Osaka, Japan. Note three worn teeth at left in descending tooth row, and broken tip of the functional first tooth at upper right. (SEM, ×450; scale bar = 100 μm.)

Figure 2. Detail of wear in tooth no. 3 in Figure 1. (SEM, ×4500; bar = 10 m.)

Figure 3. Typical long, coiled radula from 8-mm long British Columbia specimen. (SEM, ×300; bar = 100 μm.)

Figure 4. Terminal ascus with jumble of loose teeth (not coiled) noted only in a few specimens from Australia and New Zealand. From a 3-mm long specimen from Sydney, Australia. (SEM, ×300; bar = 100 μm.)

Figure 5. Detail of broken tip of tooth no. 1 in Figure 1. (SEM, ×7000; bar = 10 μm.)

Figure 6. Detail of series of seven juvenile teeth in coil of radula from 6-mm specimen, Triangle Island, British Columbia. (SEM, ×2000; bar = 10 μm.)

Figure 7. Tip of hollow penial style from 5-mm specimen from Leigh, New Zealand, showing thickened, turned up tip (arrow), typical of all *Placida dendritica* examined from Pacific and Atlantic regions. (SEM, ×7000; bar = 10 μm.)

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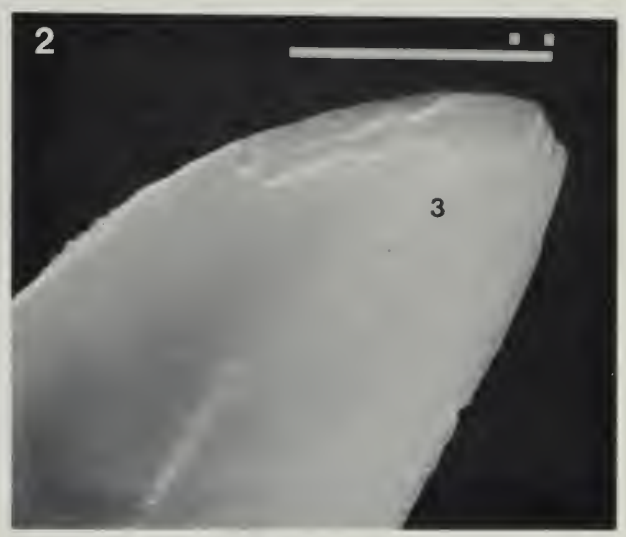
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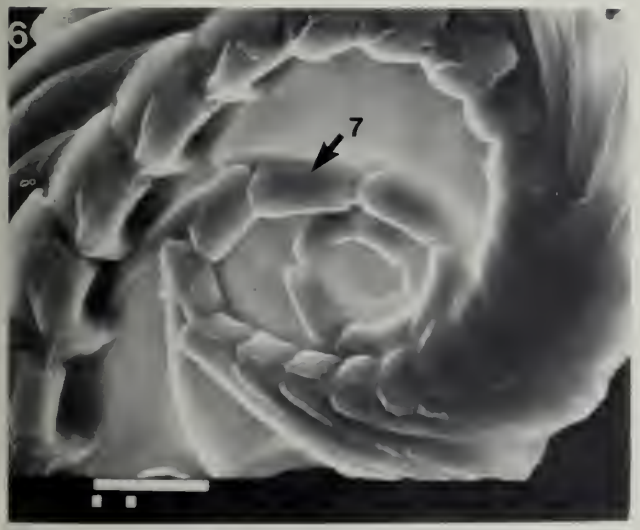
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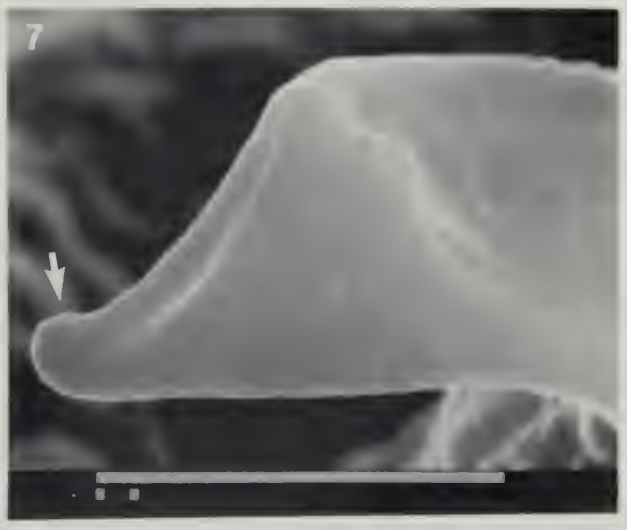
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and *Derbesia novaezelandiae* Chapman. Slugs feeding on *Derbesia* were a paler green than those from the *Codium* plants.

It is evident that *Placida dendritica* has a somewhat wider spectrum of algal prey genera than previously assumed. Its occurrence in New England and Atlantic Canada undoubtedly preceded, and was not predicated upon, the recent establishment of *Codium* in southern New England as postulated by Clark & Franz (1969).

Diversity of Habitats

Clark & DeFreese (1987) have recently emphasized that ascoglossans, as a group, are broadly distributed in latitude and habitat, seemingly unfettered by their trophic specialization. Remarkably, the same can be said of several species within that group, and *Placida dendritica* is a superb example. Perusal of available literature, however, does not reveal the truly astounding diversity of habitats from which this species can be collected. One simply learns that *P. dendritica* occurs on *Codium* and *Bryopsis* subtidally, without any mention of substrate, tidal and temperature extremes, winter ice conditions, or general description of local environs.

That malacologists may have a better understanding of the adaptive capabilities of *Placida dendritica,* and be encouraged to seek it out, the following 11 examples (from personal experience, unless otherwise noted) have been selected. To what degree these extremely different environments modify this species' growth and reproductive patterns at the geographic or regional level is unknown.

(1) Newfoundland, Avalon Peninsula, Logy Bay Marine Laboratory. Rocky coast of sheer cliffs, tidal range 0.9 to 1.9 m, too exposed and stormy for safe anchorage of research vessels, temperatures from −1.5 to 14°C with drift ice and icebergs in winter. *Placida dendritica* was found on tufts of *Derbesia marina* on valves of *Mytilus* sp. attached to rocks at a depth of 8 m.

(2) Nova Scotia, Annapolis Basin, Bear River estuary. Broad, shallow, muddy, tidal river, commercial clam digging, twice-daily tides of 7.8 to 10.2 m, ice blocks in winter. *Placida dendritica* was found in a mixed collection of algae and hydroids scraped from the surface of wood-encased, bridge piers exposed at E.L.W.S. tide.

(3) Nova Scotia, Chester Basin, Atlantic coast. Tides 1.5 to 2.2 m, seasonal temperature range of −1 to 16°C, in winter sea ice often freezes shore to shore for months. *Placida dendritica* was found on *Derbesia marina* on valves of *Modiolus modiolus* Linn. attached to rocks at a depth of 4 m.

(4) Connecticut, Noank, Mystic River estuary (Clark, 1975). *Zostera marina* Linn. dominant in bay area, *Placida dendritica* found on *Codium fragile* attached to small rocks on sand/mud bottom, attached to wooden bridge trestle, and to wooden hull of grounded ship, at depths of 0.5 m to 3 m.

(5) Florida Keys (Clark, 1975:43, no further information).

(6) Lesser Antilles, Curaçao, Piscadera Baai (Marcus & Marcus, 1970)—"From algae and *Thalassia* in outer bay."

(7) British Columbia, outer coast of Vancouver Island, Bamfield Marine Laboratory. Strong currents, rocky coast with many islands, nutrient rich waters, diverse and abundant marine flora and fauna, tidal range 2.7 to 3.9 m, and seasonal range of sea temperatures near 7 to 14°C. *Placida dendritica* was found on *Codium fragile* growing on rock faces at depths of 2 to 6 m.

(8) Japan, Honshu Island, Seto Marine Laboratory. Area of intensive tourism, fishing, agriculture, marine transport facilities, highly polluted, sea temperatures from 12 to 28°C under influence of warm Kuroshio Current, many tropical and sub-tropical species, tides to 1.8 m. *Placida dendritica* was found on tufts of *Derbesia lamourouxii* (=*marina*?) growing on the surface of tunicates attached to rocks on a bottom of sand, rock, cobble, and mud at a depth of 5 m.

(9) Australia, Sydney, south shore bays of Botany Bay. Area of immense coastal sand dunes, bay shallow, warm, with commercial oyster racks, tides from 1.2 to 1.8 m, at E.L.W. with 0.1 to 0.3 m water depth over a ripple sand substrate; shallows have *Zostera* beds while *Posidonia australis* Hook. f. grass dominates in deeper water. *Placida dendritica* was found on *Codium fragile* attached to cockles (*Cardium rackette*) buried in the sand.

(10) New Zealand, North Island, Leigh Marine Laboratory. Shore of jagged platforms of conglomerate and mudstone, with abundant pools, caves and crevices, tidal range of 2.6 to 3.5 m, sea temperature from 14 to 21°C. *Placida dendritica* was found subtidally on rock-encrusting mats of *Codium adhaerens,* and in the tide pools on *Derbesia novaezelandiae* epiphytic on the brown alga *Carpophyllum plumosum.*

(11) New Zealand, South Island, Dunedin, Portobello Marine Laboratory in Otago Harbour. A 20-km long sheltered inlet, laboratory is 8 km from entrance at the tip of peninsula jutting into the harbor, a restriction generating tidal currents of 3 to 4 knots which keep this section clear of harbor silts, harbor surface temperatures from 5 to 19°C, shore of basalt cliffs and ledges with rock fragments at cliff bases in shallow water. *Placida dendritica* found on *Bryopsis plumosa* (but not on equally abundant *Codium fragile*) attached to rocks in 0.5 m of water at E.L.W.

These 11 examples cover an impressive spectrum of habitats, but it is equally evident that several of the algal species fed upon by ascoglossans have similar, nearly global distributions. This may be relevant to the general question of why there is not more speciation within certain genera of ascoglossans. Perhaps the global constancy of this ascoglossan species is a reflection of the seemingly immutable persistence of its host plants.

Number of Teeth

Within a range of body lengths of 2 to 20 mm, the number of teeth in the ascending row varied from 6 to 18,

Table 2

Numbers of radular teeth in *Placida dendritica* relative to body length, from 10 geographic regions. NZ = New Zealand; Au = Australia; Jp = Japan; BC = British Columbia; NS = Nova Scotia; Nf = Newfoundland; Ir = Ireland; En = England; Sp = Spain; It = Italy. Figures in parentheses are conservative tooth counts, as those specimens had a compact jumble of free teeth in their ascus.

Body length (mm)	Ascending tooth row										Descending tooth row										Total number teeth									
	NZ	Au	Jp	BC	NS	Nf	Ir	En	Sp	It	NZ	Au	Jp	BC	NS	Nf	Ir	En	Sp	It	NZ	Au	Jp	BC	NS	Nf	Ir	En	Sp	It
20	8		7								38		33								46		40							
18	8										27										35									
16										7										27										34
14	10		9								29		27								39		36							
12	8		7								34		25								42		32							
12			7										29										36							
11										8										27										35
10			6										24										30							
9							8			7							37			24							45			31
8				18										54										72						
7				15			9	9						78			50	19						93			59	28		
7				15				10						40				25						55				35		
7								8										21										29		
7								8										22										30		
7								8										22										30		
7								10										19										29		
6	10			13				10			28			48				21			38			61				31		
6				15										37										52						
5	13		7	13		10					30		24	33		20					43		31	46		30				
5				10										29										39						
4	13	12			10						30	(42+)			24						43	(35+)			34					
4	13	13									31	(22+)									44	(54+)								
4	15										(38+)										(50+)									
4	10										(38+)										(48+)									
4	11										25										36									
3		13						11				24						18				37						29		
3		14										21										35								
3		12										28										40								
3		9										30										39								
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3		13										26										29								
3		12										23										35								
3		13										23										36								
3		10										(30+)										(40+)								
3		10										31										41								
3		14										31										45								
2					6				8						28				21						34				29	
2									8										22										30	
2									8										23										31	
2									10										33										43	

Specimen totals: 11 NZ, 13 Au, 6 Jp, 4 BC, 2 NS, 1 Nf, 2 Ir, 8 En, 4 Sp, 3 It = 54 total.

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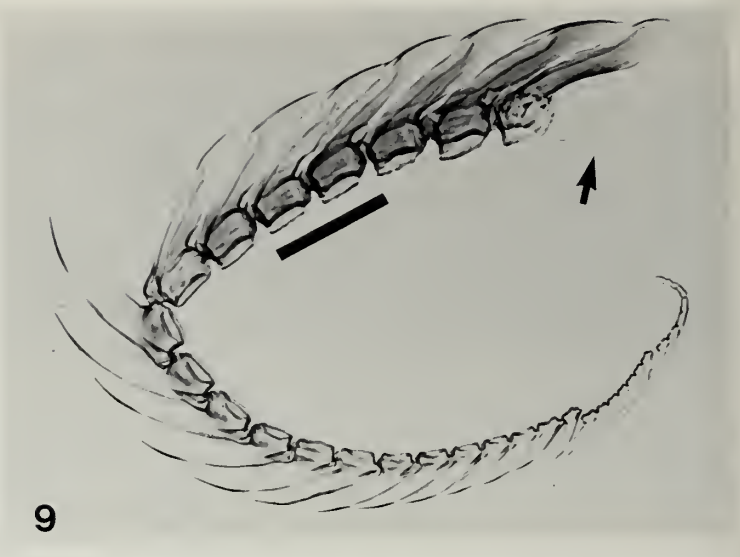
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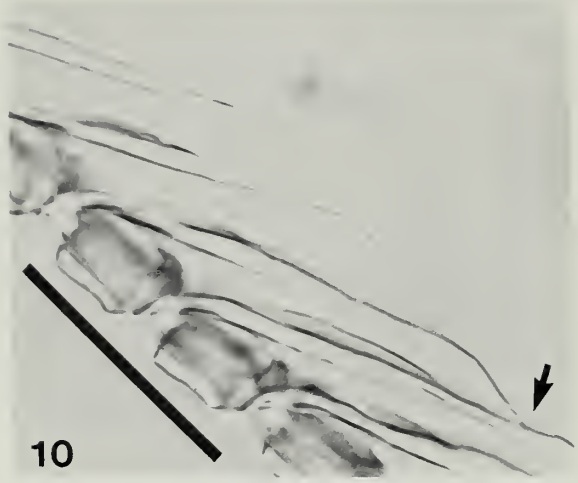
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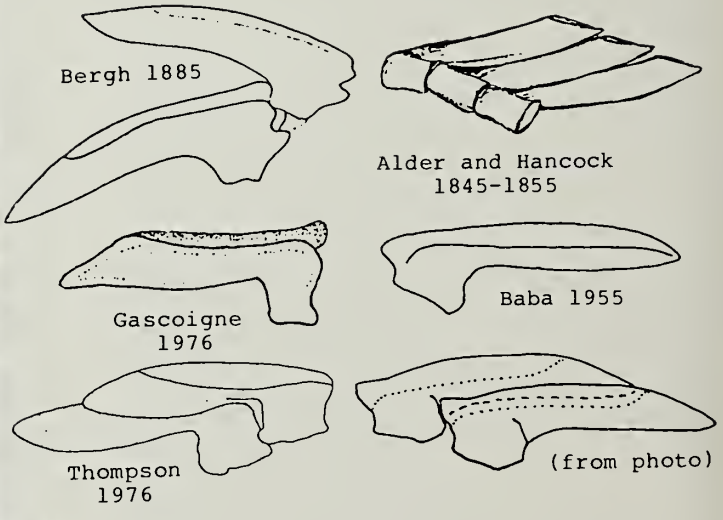

Bergh 1885
Alder and Hancock
1845-1855
Gascoigne
1976
Baba 1955
Thompson
1976
(from photo)
13

in the descending row (including ascus) from 18 to 78, and total individual counts from 28 to 93 teeth. The latter two counts were both from 7-mm long specimens. There was a thoroughly perplexing absence of positive correlation between body length and number of teeth, for most of the higher and all of the highest tooth counts are from specimens 8 mm or less in length. The greatest discrepancy within one sample was between the larger and smaller New Zealand specimens (Table 2). However, all the larger animals came from Otago, South Island, whereas the smaller ones were collected at Leigh on North Island. Is this north-south difference (particularly the low number of teeth in the ascending row of the large individuals) true for other populations on the two islands, or was this a temporal phenomenon similar to the fluctuating tooth counts reported for *Elysia chlorotica* (RAYMOND & BLEAKNEY, 1987)?

Other interesting geographic variations noted were (1) the occasional occurrence of a jumble of loose teeth in the ascus, instead of a neat coil, noted only in Australia and New Zealand (6 of 24 specimens examined) and (2) the highest tooth counts and the largest terminal radular coils limited to British Columbia.

Radular Morphology

Figure 8 is a photomicrograph of an entire buccal mass showing ascending (dorsal) tooth row, and descending (ventral) tooth row in which the teeth progressively decrease in size. The production of new teeth is evident in Figure 9 in the ascending tooth row where two insubstantial "ghost teeth" commence the series. Two such translucent teeth was the norm for most specimens of *Placida dendritica,* and these were included when counting teeth.

The descending radular limb is long, and usually continuous, terminating in a series of 5 to 7 juvenile teeth (GASCOIGNE & SARTORY, 1974) which lack fully formed, pointed, cusps on their blocklike bases (Figures 6, 9). This terminal region (in all of the geographic regions sampled) may have the configuration of a long curve (Figure 9), or be sharply hooked (Figure 8), or tightly coiled (Figures 3, 6). The classic ascoglossan sac, in which all discarded teeth are deposited forming a jumbled mass, was observed only in Australian and New Zealand specimens, where 25% of those examined (6 of 24) had an ascus sac with a jumble of teeth (Figure 4). The only potential example of loose teeth in an ascus from another geographic area, Europe, seems to be BERGH (1885:pl. V, fig. 6). However, I believe his diagram depicts a typical coil, because there are seven block-shaped teeth prior to the first strongly cusped tooth. Those extremely small, cusped teeth he included in the ascus must have been an optical artifact because *Placida dendritica* does not produce teeth that small with distinct bases and cusps. Bergh's other diagram of a radula of this species (pl. II, fig. 2) is of the typical hook-shaped, descending limb.

The morphology of individual teeth varies from straight to slightly down-curved, and the tips may be rounded, pointed, or angular. However, to determine these shapes is difficult and requires care, because a slight shift of the viewing angle (whether light microscopic or SEM) generates new proportions. An additional pitfall is that unless the teeth being examined are of the ascending row, and thus not yet used in feeding, the effect of attrition so often evident on teeth in the descending limb can create misleading outlines. Subtle differences in proportions can be detected by comparing Figures 10 and 11, where tips of the unused ascending teeth are pointed and fit closely into the pocket of each succeeding tooth, but are worn and rounded and slightly shorter in the descending tooth row (Figure 11).

Of the seven authors who have published diagrams of individual teeth, by far the best representation is that of BERGH (1885). His diagram and those of other selected authors are assembled in Figure 13, as well as a new diagram based on the present study. The two most confusing aspects of those previous diagrams are a conse-

←

Explanation of Figures 8 to 13

Figure 8. Entire buccal mass from *Placida dendritica,* Chester Basin, Nova Scotia, photographed after 15 min in tissue solubilizer. Note mouth (m), esophagus (e), ascending tooth row (a) originating at large generative sac (g), and descending tooth row (d) with terminal coil of juvenile teeth. (Scale bar = 200 μm.)

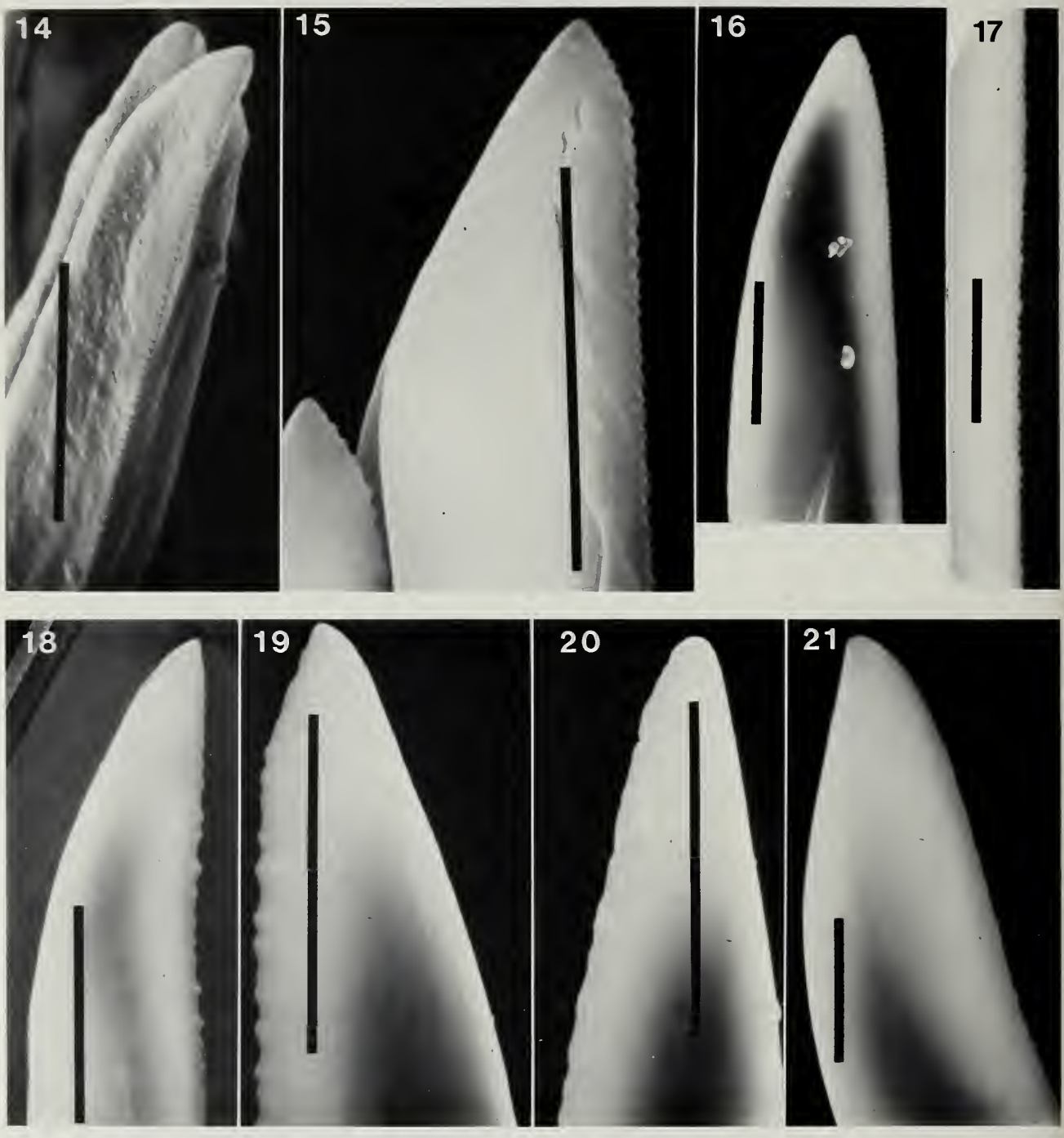
Figure 9. Radula and remnants of buccal mass of an 1866 Naples, Italy, specimen, after overnight in tissue solubilizer at 35°C. In the ascending tooth row, top of photo, are six fully formed teeth, one nearly differentiated, and ghostly outlines of two others. These "ghost teeth" (arrow) were included in the totals of numbers of teeth in the ascending rows listed in Table 2. (Scale bar = 60 μm.)

Figure 10. New, unused teeth in the ascending tooth row of an Osaka, Japan, specimen showing pointed tips closely fitted (arrow) into dorsal groove of adjacent tooth. (Scale bar = 81 μm.)

Figure 11. Three worn and broken teeth within the descending tooth row of the same radula as Figure 10.

Figure 12. Top of hollow penial style embedded in apex of penis (p) showing thickened, hooked lip (arrow) not previously reported but common to all specimens of *Placida dendritica* examined. Specimen from Otago Bay, New Zealand. (Scale bar = 20 μm.)

Figure 13. Five examples of the diversity of published illustrations of tooth morphology for *Placida dendritica,* with a sixth diagram traced from a photomicrograph of the ascending tooth row of a 9-mm specimen from Ireland. In that diagram (a lateral view) the dotted lines represent the depth of the dorsal trough and the dash line represents the serrated keel edge of the upper tooth fitted into the trough.



Explanation of Figures 14 to 21

Figures 14 to 17 are representative of radulae from the Pacific Ocean region, whereas Figures 18 to 21 are typical of specimens from the North Atlantic Ocean and Mediterranean Sea.

Figure 14. Ventral aspect of serrated edge on keel of radular tooth of 4-mm *Placida dendritica,* Sydney, Australia. (SEM, ×4500; scale bar = 10 μm.)

Figure 15. Lateral aspect of serrated edge of tooth from 4-mm long specimen, Sydney, Australia. (SEM, ×7000; bar = 10 μm.)

Figure 16. Lateral aspect of tooth from 6-mm specimen, Triangle Island, British Columbia. (SEM, ×3000; bar = 10 μm.)

Figure 17. Keel edge of 21-mm long specimen, Otago Bay, New Zealand. (SEM, ×3000; bar = 10 μm.)

Figure 18. Serrated edge of unused tooth from ascending row of 8-mm long *Placida dendritica,* Loo, England. (SEM, ×4500; bar = 10 μm.)

quence of (1) representing the bottom of the deep trough in a tooth (lateral view) as a solid line and thus implying a surface feature, rather than as a dotted line indicating a visible, subsurface feature, or (2) unnecessarily indicating the transition from lateral wall to medial keel (Figure 14) by a full-length line.

A significant tooth feature, not reported previously, is the serrated cutting edge common to all populations examined. BABA (1955) and JENSEN (1980) reported the teeth of *Placida dendritica* to be smooth edged. THOMPSON (1988) noted a "roughened" cutting edge "but not regularly denticulate" on two Mediterranean specimens from Yugoslavia. The serrations revealed by my SEM examinations are of two types, and one was limited to the Pacific Ocean samples and the other to the Atlantic Ocean and Mediterranean Sea. The serrations of all Pacific region samples are of a rather uniform series of adjacent projections, square to rectangular in outline, with a truncate to rounded free edge (Figures 14–17). The Atlantic and Mediterranean specimens have irregularly spaced, larger, sharply pointed serrations, somewhat conical with the base of the cone extending as a ridge a short distance up the side of the tooth keel (Figures 18–21).

In absolute terms, this difference in serrated edging is rather miniscule, but it is interesting that specimens from the Pacific Ocean rim differ as a group from samples from North Atlantic and Mediterranean shores. Assuming this indicates that Atlantic and Pacific populations of *Placida dendritica* have long been isolated, then one can pose pertinent zoogeographic questions about southern Africa and the Caribbean Sea. Although climatically disjunct today, there are coastal areas in southern Africa where 17 to 20% of the opisthobranch species also occur in the northern Atlantic and where less than 2% are Indo-Pacific (GOSLINER, 1987). Gosliner calculated that of the probable sister species of endemic opisthobranchs in southern Africa, 43% are known from the northern Atlantic. *Placida dendritica* has not yet been reported from southern Africa but, if it is, the tooth serrations should have the same configuration as European populations, assuming the conclusions drawn from data in the present paper are valid. The Caribbean Sea is also of special zoogeographic interest, for examination of a series of specimens of *P. dendritica* from several areas in that region could answer the intriguing question of whether those populations have an original North Atlantic or a more recent Pacific Ocean affinity.

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Figure 19. Serrated edge of tooth from another Loo specimen. (SEM, ×7000; bar = 10 μm.)

Figure 20. Worn serrated edge of a used tooth from descending tooth row of same radula as Figure 19. (SEM, ×7000; bar = 10 μm.)

Figure 21. Tooth extracted from 9-mm specimen, after 122 yr in preservation, collected near Naples, Italy, in 1866. (SEM, ×3000; bar = 10 μm.)

Penial Style Morphology

Examination of the minute, hollow, penial style under the light microscope and with SEM revealed a terminal, thickened, slightly upturned projection (Figures 7, 12), not depicted previously in diagrams by GASCOIGNE (1974) for a British sample nor by THOMPSON (1973) for an Australian specimen.

Gut Tract Branching Pattern

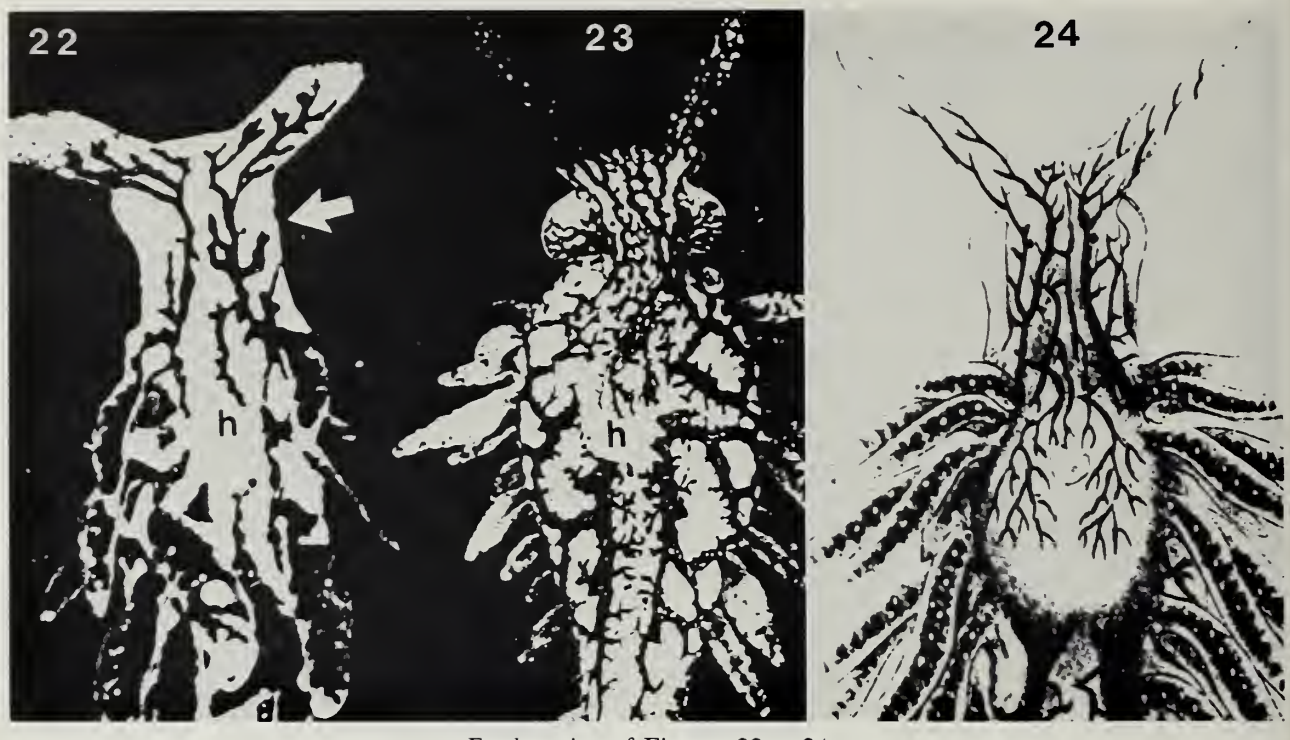
From my collection of color transparencies of live *Placida dendritica,* and one donated by A. Kress, a set of enlarged color prints were produced and comparisons made of the branching pattern of the green gut tract of specimens from New Zealand, Australia, Japan, British Columbia, Nova Scotia, Newfoundland, and England. No appreciable differences were detected. Even the basic asymmetry of branching in the heart-head region was identical. In this body region, there are major medial branches to the heart and head, and one lateral branch to the gonopore area, all originating from the right gut tract. This pattern is obvious in small specimens of 2 to 5 mm body length (Figure 22) and can readily be deciphered in larger individuals in spite of subsequent gut branch multiplication and anastomosing (Figure 23).

Most diagrams of the gut tract of *Placida dendritica* in the literature seem based upon ALDER & HANCOCK (1845–1855:fam. 3, pl. 40) which upon close examination reveals an invented bilateral symmetry as well as bifurcating, sharply pointed, terminal branches imposed upon the original print sheet by the color illustrator's delicate brush strokes (Figure 24). The real asymmetry is evident in published color photos of a British specimen (THOMPSON, 1976) and one from California (BEHRENS, 1980). Rather interestingly, MACFARLAND (1966) described this asymmetry in detail in his text (p. 40) but obscured it in his pl. 4, fig. 3 by illustrating the specimen from the left lateral aspect.

SUMMARY

Placida dendritica is a cosmopolitan, conservative ascoglossan species with reportedly identical features in Atlantic and Pacific Oceans and in Northern and Southern Hemispheres. However, examination of radulae from 10 geographic areas revealed two types of serrated edge on the teeth: one type was limited to the Pacific Ocean Basin and the other to the Mediterranean Sea and North Atlantic.

Within a range of body lengths of 2 to 20 mm, the number of teeth in the ascending row varied from 6 to 18, in the descending row (including ascus) from 18 to 78, and total individual counts from 28 to 93 teeth. There is a thoroughly perplexing absence of positive correlation between body length and number of teeth, for most of the higher and all of the highest tooth counts are from specimens 8 mm or less in size.



Explanation of Figures 22 to 24

Figure 22. Branching gut tract of 5-mm *Placida dendritica,* Logy Bay, Newfoundland. Arrow points to pair of tiny eyes. Posterior to the right eye are three major branches springing from the large right anterior gut tract: one medial branch pointing forward to the head; another medial, posterior to the first, and directed towards and onto the heart (h); and a large lateral, nearer the eye, directed towards the gonopore area (same arrow).

Figure 23. Gut tract of 7-mm specimen, Seto, Japan, demonstrating degree of expansion of branching pattern in larger specimens, but with the basic asymmetry of Figure 22 still evident.

Figure 24. Enlargement of color plate from ALDER & HANCOCK (1845–1855) revealing illustrator's invented elements of bilateral gut tract symmetry and his neat but imagined bifurcating pattern and finely tapered terminal branches.

An additional algal genus, *Derbesia,* has been added to the two previously reported algal genera (*Codium* and *Bryopsis*) upon which *Placida dendritica* is known to feed and spawn.

Descriptions of 11 contrasting collection sites indicate the broad spectrum of habitats in which this single ascoglossan species can be found.

Penial style morphology showed no geographic variation, but not previously reported is a small terminal projection.

The branching pattern of the gut tract appeared very conservative, even to the asymmetrical origin of three distinct branches from the right anterior tract that terminate on the head, heart, and gonopore areas respectively. This asymmetry was not evident in drawings from the literature, but was evident in published color photographs.

ACKNOWLEDGMENTS

The author is indebted to the National Sciences and Engineering Research Council of Canada for financial support over several decades, and he sincerely thanks the many individuals at museums, marine laboratories, and universities who have so kindly assisted this ascoglossan adventurer.

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First Record of the Nudibranch *Trapania brunnea* Rudman in New Zealand Waters with Comments on Intraspecific Variation in the Species

by

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Abstract. *Trapania brunnea* Rudman, 1987, is newly recorded from New Zealand on the basis of six specimens discovered together at the Poor Knights Islands off the Northland coast. The opportunity is taken to describe intraspecific variation as regards coloration of the body, foot, anterior foot extensions, rhinophores, gills, and lateral body processes in this distinctive species. *Trapania brunnea* is the eleventh nudibranch species to be recognized as possessing a natural trans-Tasman distribution.

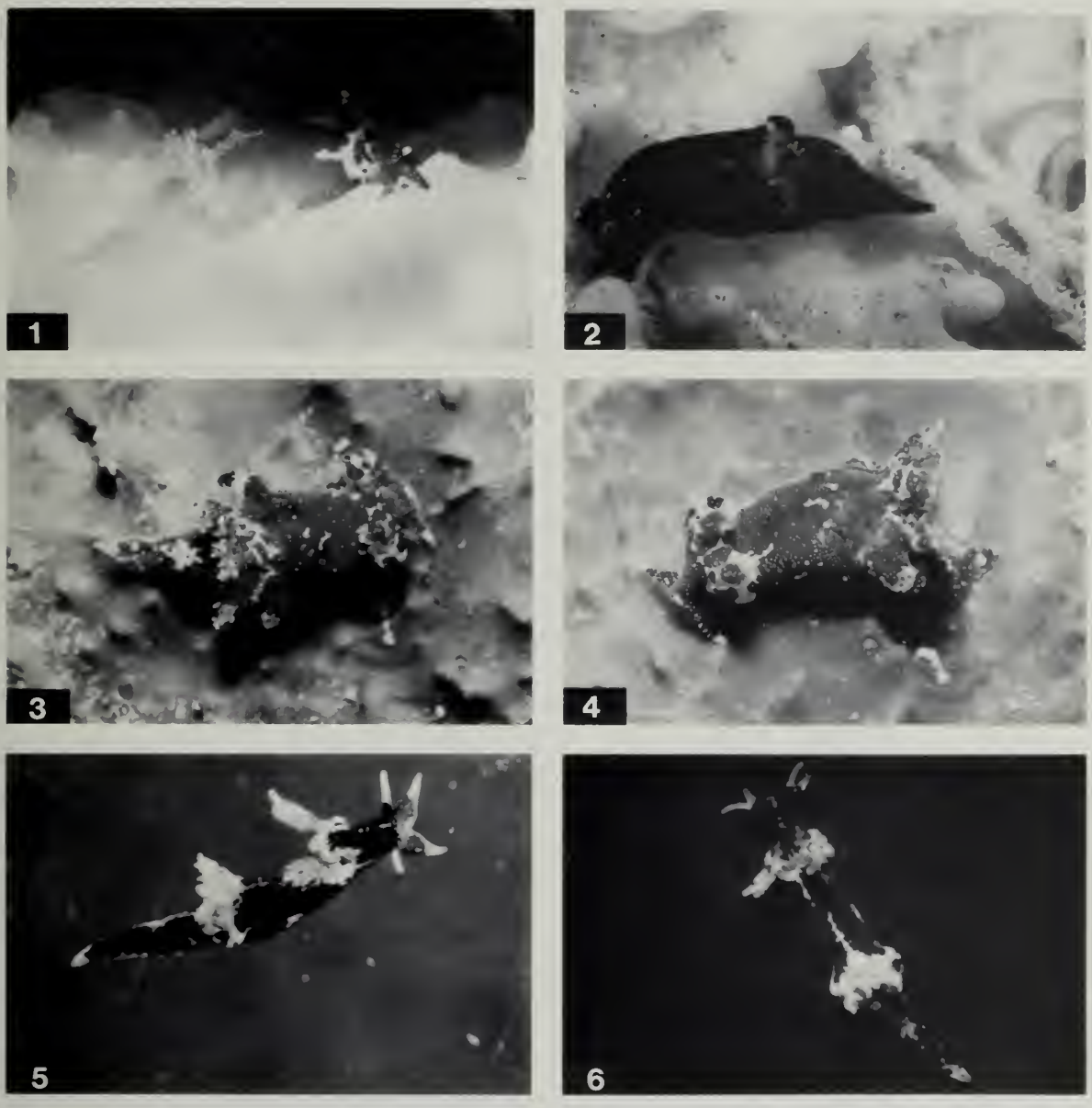
The dorid nudibranch *Trapania rudmani* Miller was the first described, and hitherto supposedly only, member of its genus from New Zealand (MILLER, 1981; RUDMAN, 1987). It is certainly endemic to that country (WILLAN & COLEMAN, 1984; WILLAN & MORTON, 1984). On 12 May 1988, Dr. P. Chapman-Smith observed and photographed six specimens of a second *Trapania* species, *T. brunnea* Rudman, 1987, in 14 m in a recess on one of the walls of Barren Arch on the eastern side of Tawhiti Rahi, the largest island of the Poor Knights group off Northland's east coast. Two of Dr. Chapman-Smith's photographs are reproduced here (Figures 1, 2).

The New Zealand specimens ranged in size from 12 to 15 mm crawling length. Because the maximum length previously reported was 17 mm (RUDMAN, 1987), I assume all the New Zealand specimens were sexually mature.

All six specimens were together on one clump of the bulky, encrusting, white sponge *Cacospongia* sp. (Dictyoceratida: Thorectidae). Dr. Chapman-Smith noted that some of the *Trapania brunnea* appeared to be feeding on this sponge and that there was a spawn mass (visible on the right in Figure 2) on the sponge surface; this spawn could have been laid by one of the animals.

The New Zealand specimens were not collected, but because *Trapania brunnea* is distinctive and wide ranging in temperate Australian waters, positive identification is possible on the basis of the photographs alone. Actually the New Zealand specimens vary less in coloration from the original description than some eastern Australian animals I have examined. RUDMAN's (1987) description mentioned color variation in the amount of white pigmentation on the body and foot. However, it is apparent, both from the present New Zealand specimens and my Australian material, that variation also exists in coloration of the anterior foot extensions, rhinophores, gills, and lateral body processes. This intraspecific variation needs to be described to fully comprehend the species and to avoid disagreements over specific identifications as have happened with European *Trapania* species (*e.g.*, PRUVOT-FOL, 1954; HAEFELFINGER, 1960; THOMPSON & BROWN, 1984). The following account of color variation encompasses the New Zealand specimens as well as two from eastern Australia, one each from northern New South Wales (Figures 3, 4) and southern Queensland (Figures 5–7).

The ground color is always uniform, dark chocolate brown, and there is a regular peppering of either numerous (Figures 3, 4) or sparse (Figures 5–7) white specks. A very irregular white streak extends the length of the body along the dorsal midline. This streak is usually present as a narrow line on the head, but it can be represented by a series of interrupted dashes (Figures 5–7), or merely a simple relatively small white patch (Figures 3, 4). The median streak stops at the level of the rhinophores where there is a prominent, relatively broad, white streak extending both anteriorly and posteriorly; sometimes the streaks from both sides coalesce in the midline to produce an H pattern. The median streak usually commences again over the pericardium at the level of the termination of the streaks extending posteriorly from the rhinophores (Figures 6, 7) but there can be considerable separation (Figures



Explanation of Figures 1 to 6

Figures 1, 2. *Trapania brunnea*; lengths 14 mm and 15 mm respectively. From 14 m, Tawhiti Rahi Island, Poor Knights Islands, Northland, New Zealand, 7 May 1988. Photographs: P. Chapman-Smith.

Figures 3, 4. *Trapania brunnea*; length 13 mm. From 21 m, Split Solitary Island, northern New South Wales, Australia, September 1986. Photographs: C. Buchanan.

Figures 5, 6. *Trapania brunnea*; length 8 mm. From 2.5 m, Myora spit, Moreton Bay, southern Queensland, Australia, 2 March 1982. Photographs: R. C. Willan and J. C. Paterson respectively.

1, 2), or the median and lateral streaks may be absent altogether (Figures 3, 4). The median streak is widest and most irregular in shape behind the gills, even forming an elongate white blotch in some individuals (Figure 3). The tip of the tail is always white.

The foot has a thin, irregular, white marginal line that is expanded into a white blotch on either side in front of, and behind, the gills. The tentaculate anterior corners of the foot have a brown proximal section, which is white spotted, and a translucent white distal section (Figures 5–7). The latter section may, however, be reduced to an apical white spot (Figure 1) as occurs on the oral tentacles.

The rhinophores have a translucent white stalk and chocolate (Figures 1–4) or translucent white (Figure 5) clavus with white spots on the lamellae. The apex of the rhinophores is white.

Figure 7

Trapania brunnea; length 8 mm. From 2.5 m, Myora spit, Moreton Bay, southern Queensland, Australia, 2 March 1982. Specimen drawn from life by the author.

The axes and pinnules of the gills are either translucent brown (Figures 1–4) or translucent white (Figures 5–7) with white specks similar to those on the body.

The lateral extra-rhinophoral and extra-branchial appendages have, successively, a brown base, irregular translucent white central section, brown distal section, and white apex. Both brown sections are peppered with white specks. The brown distal section can be reduced to a blotch, but I have never seen a specimen in which it could be described as a median band as was indicated in the original description.

Trapania brunnea was previously reported from South Australia, Tasmania, Victoria, central New South Wales, and Lord Howe Island (RUDMAN, 1987), and I have Australian material from northern New South Wales (Figures 3, 4) and southern Queensland (Figures 5–7). The occurrence of *T. brunnea* in northeastern New Zealand is significant biogeographically because it represents another nudibranch with a trans-Tasman distribution, *i.e.*, a species common to temperate Australia and northern New Zealand waters and not naturally occurring elsewhere. The other examples I know of are *Plocamophorus imperialis* Angas, *Tambja verconis* (Basedow & Hedley), *Okenia pellucida* Burn, *Archidoris wellingtonensis* (Abraham), *Doriopsis flabellifera* (Cheeseman), *Chromodoris amoena* Cheeseman, *Dermatobranchus pulcherrimus* Miller & Willan, *Tularia bractea* (Burn), *Spurilla australis* Rudman, and *Aeolidia helicochorda* Miller. Such shared species constitute approximately 7% of New Zealand's and 3% of temperate eastern Australia's total nudibranch fauna. I interpret the higher percentage for New Zealand as a result of that country's insularity, geographical isolation, relatively small area, and generally colder waters. In all probability there are some additional unrecognized trans-Tasman nudibranch species, but their detection will be hampered by their small size and the inadequate knowledge of the eastern Australian fauna.

ACKNOWLEDGMENTS

Had Dr. P. Chapman-Smith not shown me his slides, the presence of *Trapania brunnea* in New Zealand would have gone unrecognized. I am sincerely grateful to him, to Mrs. C. Buchanan and Mr. J. Paterson for allowing me to reproduce their original photographs of *T. brunnea* in this paper. In kindly identifying the sponge, Dr. C. Battershill commented that it was an undescribed species that he had only seen at the back of submarine caves.

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Kelliella elegantula sp. nov., First Record of the Genus from British Columbia, Canada (Bivalvia: Kelliellidae)

by

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Abstract. *Kelliella* ***elegantula*** sp. nov. is proposed for a specimen taken in 1760 m near Triangle Island, British Columbia. It is the first record of the genus from British Columbia. Survey of the genus reveals a uniform conchology, but two anatomical types, suggesting that abyssal and hadal species be separated from the shallow-water species.

The genus *Kelliella* Sars, 1870 (=*Kellyella* Fischer, 1887, *nom. null.*), includes 14 species of small and usually deep-water bivalves. The type of the genus is *K. abyssicola* Sars, 1870, which occurs in the northeast Atlantic Ocean from Norway to West Africa and the Mediterranean Sea in 40 to 1200 m. The species was soon synonymized with *Venus*(?) *miliaris* Philippi, 1844, a Tertiary fossil of Italy. This was confirmed by comparison of topotypes with living material from Norway (ODHNER, 1960). The genus clearly belongs to the order Veneroida. The hinge is feeble and probably neotenous, and lateral teeth are absent. Usually assigned to the superfamily Arcticacea Newton, 1891, which conclusion is supported by the gross anatomy, particularly the gill, and structure of the alimentary canal, which is basically similar to that described in *Glossus humanus* (Linnaeus, 1758) by OWEN (1953) and reviewed by PURCHON (1987). The shell structure of *K. miliaris* is entirely aragonitic, with a poorly differentiated outer layer and a thin complex crossed-lamellar inner layer. This structure is similar to some representatives of the Glossacea and Arcticacea (TAYLOR *et al.*, 1973). The genus is placed in the family Kelliellidae Fischer, 1887, together with several extinct Eocene and Oligocene genera that are only doubtfully related, and two living Indo-Pacific genera that on conchological grounds can only be doubtfully included in the family.

All the species of *Kelliella* are small to minute and generally confined to abyssal and hadal depths. The conchological characters are remarkably uniform, but significant anatomical differences suggest that those species with a single pallial fusion and a greatly hypotrophied gill outer demibranch, typified by the type of the genus, may be separated at the generic level from the deep-water species with inhalant and exhalant apertures, and only slightly

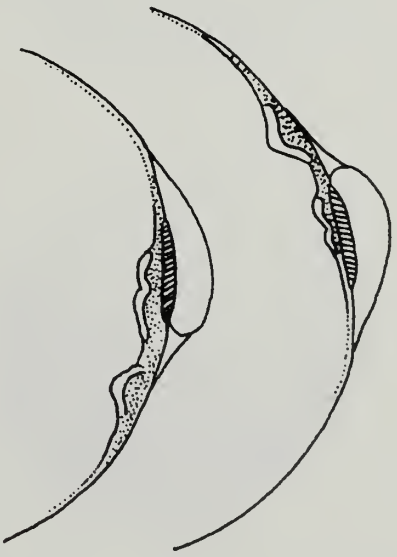

Figure 1

Kelliella ***elegantula*** Bernard, sp. nov. Interior view of right and left hinge.

Table 1

Living species of the genus *Kelliella*

Species	Location	Depth (m)
**Callocardia*(?) *adamsi* E. A. Smith, 1885	Northeast Pacific	4410
**Callocardia*(?) *atlantica* E. A. Smith, 1885	Sierra Leone	1860
†*Vesicomya brunni* Filatova, 1969	Kermadec Trench	9000
†*Kelliella* ***elegantula*** sp. nov.	Northeast Pacific	1760
†*Kelliella galathea* Knudsen, 1970	Eastern Pacific	3570
Kellyella goesi Odhner, 1960	West Indies	360–540
†*Kelliella indica* Knudsen, 1970	Indian Ocean	4350
Venus(?) *miliaris* Philippi, 1844	Northeast Atlantic	50–1200
**Kelliella nakayamae* Habe, 1953	Pleistocene Japan	
**Kelliella nitida* Verrill, 1885	Northwest Atlantic	3800
†*Callocardia*(?) *pacifica* E. A. Smith, 1885	Mid north Pacific	5394
**Diplodonta pilula* Dall, 1881	Caribbean Sea	570
†*Kelliella sundaensis* Knudsen, 1970	Sunda Trench	6900
†*Kelliella tasmanensis* Knudsen, 1970	Tasman Sea	4400

* Anatomy not known.

† Species with separated inhalant and exhalant apertures.

Figure 2

Kelliella ***elegantula***. Photograph of exterior of left valve and interior of right valve. Holotype specimen length 3.9 mm (BCPM 979-5440).

reduced outer demibranchs. The necessity of this course will be established when the anatomy of more species has been surveyed.

Kelliella ***elegantula*** Bernard, sp. nov.

(Figures 1–3)

Original description: Shell small, globose, thin and hyaline, subequilateral, equivalve. Commissure without gape. Umbones prosogyrate, prominent. Anterior dorsal margin arched. Surface with equidistant concentric rounded riblets, interspaces narrow and deep. Riblets prominent on ventral part of disc and crenulating the inner shell surface. Periostracum polished, thin, and adherent. Lunule wide and demarcated by an incised line. Escutcheon absent. Ligament short, opisthodetic, external but sunk in groove.

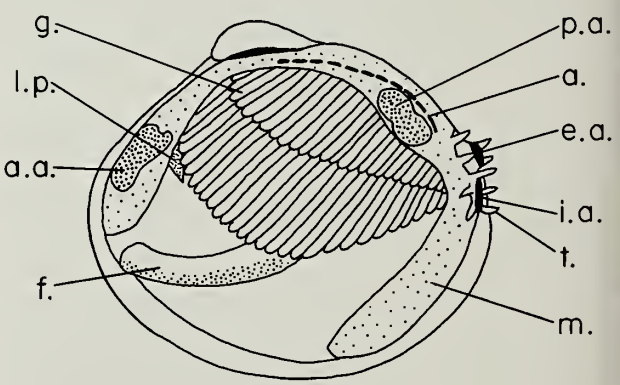

Figure 3

Gross anatomy of *Kelliella* ***elegantula*** with mantle partially removed, as seen from the left side. Abbreviations: a., anus; a.a., anterior adductor muscle; e.a., exhalant aperture; f., foot; g., gill; i.a., inhalant aperture; l.p., labial palp; m., mantle; t., tentacle.

Hinge plate narrow and delicate, dentition feeble. Each valve with short triangular anterior pseudocardinal tooth and longer reflexed posterior pseudocardinal tooth. Adductor muscle scars subequal and rounded. Pallial line entire, obscure.

Type locality: West coast of Triangle Island, British Columbia at 50°54.5'N, 130°12.0'W in 1760 m. Collected by D. B. Quayle, Fisheries & Ocean Station 63-211 on 11 September 1964.

Holotype: The dimensions of the holotype are length 3.9, height 3.7, width 2.4 mm. The unique type is deposited in the British Columbia Provincial Museum, Victoria, Canada (BCPM 979-5440).

Etymology: The specific name is derived from the Latin *elegans,* meaning "choice" and "beautiful," referring to the elegance of the shell.

Anatomy: The specimen was fixed in alcohol and dried. After rehydration the following anatomical observations could be made. Exhalant aperture with short collarlike siphon. The inhalant aperture a simple slit. Apertures with 6 thin tentacles. Foot digiform, with obscure byssal groove, but no appearance of a functional byssus. Gills large and thickened, flat, heterorhabdic, inner demibranch larger. Labial palps small, upper pair joined to form an overhanging oral hood. Stomach globular, with large dorsal hood and extensive gastric shield. Major and minor typhlosoles prominent. Mid-gut and style pouch conjoined. Ducts to the digestive diverticula in three groups. Intestine direct, passing through the ventricle of the heart. Anus projecting as a long simple papilla.

Comparisons: The new species is readily distinguished from the other Pacific Ocean representatives by the more robust dentition, similar to that of *Kelliella miliaris* as described by Clausen (1958), but it differs from that species by the separate inhalant and exhalant apertures, the absence of hypertrophy of the inner mantle fold of the pedal opening, the more nearly equal demibranchs, the digiform foot lacking a heel, and the absence of the bundle of cilia on the anal papilla. The new species is superficially similar to *K. goesi* (based on illustration, holotype probably in the Naturhistoriska Museet, Sweden) but lacks the characteristic external punctae, and the sculpture is more subdued. There is some resemblance to *K. galathea* (holotype in the Zoological Museum, University of Copenhagen) which lacks the triangular anterior pseudocardinal tooth, and the shell is thinner and more inflated.

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California Late Cretaceous Donaciform Bivalves

by

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Abstract. California donaciform bivalves of Late Cretaceous age occur sporadically, but locally abundantly, in coarse-grained sandstone. Where abundant, they indicate near strand-line deposition. Seven species are allocated among a new genus, ***Adelodonax,*** and a new subgenus, ***Aliodonax,*** in the Donacidae and a new genus, ***Califadesma,*** in the Mesodesmatidae. The donacids are *Notodonax* (***Aliodonax***) ***hsui*** sp. nov. of Santonian age, *N.* (***A.***) ***bolsae*** sp. nov. of Campanian age, ***Adelodonax tectus*** sp. nov. of Santonian age, and ***A.*** *altus* (Gabb, 1864) of Maastrichtian age; the mesodesmatids are ***Califadesma aspris*** sp. nov. of Coniacian age, ***C. elaphium*** sp. nov. of Santonian age, and ***C. tuscanum*** sp. nov. of Campanian age.

Mactropsis Conrad, 1854, is a mactrid rather than a mesodesmatid. *Myadesma* Clark, 1922, is an anomalodesmacean and *Ceroniola* Wilckens, 1904, may be a donacid; both are excluded from the Mesodesmatidae and from the Mactracea.

INTRODUCTION

Although donacid bivalves have been recognized elsewhere in the Cretaceous, neither donacids nor mesodesmatids have previously been recorded from the California Cretaceous. Abundant donaciform bivalves from the Musty Buck Member of the Chico Formation at about 44 m above the base of the section on Chico Creek, Butte Co., California, proved, upon exposure of hinge lines, to belong to three genera in the Donacidae and Mesodesmatidae.

Cretaceous Donacidae include *Notodonax* (Feruglio, 1936) from the Maastrichtian of Argentina, and *Protodonax* (Vokes, 1945) proposed for species of Albian through Maastrichtian age from the Western Interior and Atlantic Coast of North America as well as the Aptian of Lebanon. Stephenson (1952) added two Cenomanian species from the Gulf Coast to *Protodonax*. The family has thus been recognized in the Early Cretaceous. The five California species herein added to the family range in age from Santonian to Maastrichtian. These species are more similar to Maastrichtian species from Chile and Argentina than to species described by Vokes (1945) and Stephenson (1952) from North America and the Near East.

The earliest mesodesmatid listed in the *Treatise on Invertebrate Paleontology* (Keen *in* Moore, 1969) is *Ceroniola* Wilckens, 1904, from the Quiriquina Formation of Late Cretaceous age. Wilckens (1904) apparently placed *Ceroniola* in the Mesodesmatidae because he considered the triangular depression beneath the beaks to be a resilifer, but the hinge teeth of *Ceroniola* show no relationship to those of *Mesodesma* Deshayes, 1832. *Ceroniola* is, as indicated by Beu (1971:124), an improbable ancestor for *Mesodesma.* Similarities between *Ceroniola* and ***Adelodonax*** gen. nov. suggest that *Ceroniola* may be a donacid.

The next oldest purported mesodesmatid (Keen *in* Moore, 1969) is *Mactropsis* Conrad, 1854, from the Eocene of Alabama. Dall (1898:907) placed *Mactropsis* in the Mesodesmatidae because it has a very thick shell. He inferred that mesodesmatids were unlikely to be recognized earlier than Tertiary because of the stage of hinge development in *Mactropsis,* but *Mactropsis* appears more closely related to the mactrid *Spisula* Gray, 1837, than to *Mesodesma.*

The next younger genus included by Keen (*in* Moore, 1969) in the Mesodesmatidae is *Myadesma* Clark, 1922, of Eocene to Miocene age from the Pacific Northwest. The lack of striated laterals and the probable lithodesma (Clark, 1922) found within its chondrophore are sufficient to exclude it from Mesodesmatidae. Beu (1971) agrees with Clark (1922) in placing it in Myadesmatidae but retains this family within the Mactracea. The rough and lamellar shell texture of *Myadesma* is more like that of *Entodesma* (*Agriodesma*) *saxicolum* Baird, 1863, of the Lyonsiidae, and the hinge structures resemble those of Periplomatidae. The tooth beneath the beak in each valve was interpreted as a cardinal by Beu (1971), but these are unduly inconstant for veneroid cardinal teeth and are not of mactracean form. Myadesmatidae has more in common with the anomalodesmacean families Lyonsiidae and Periplomatidae.

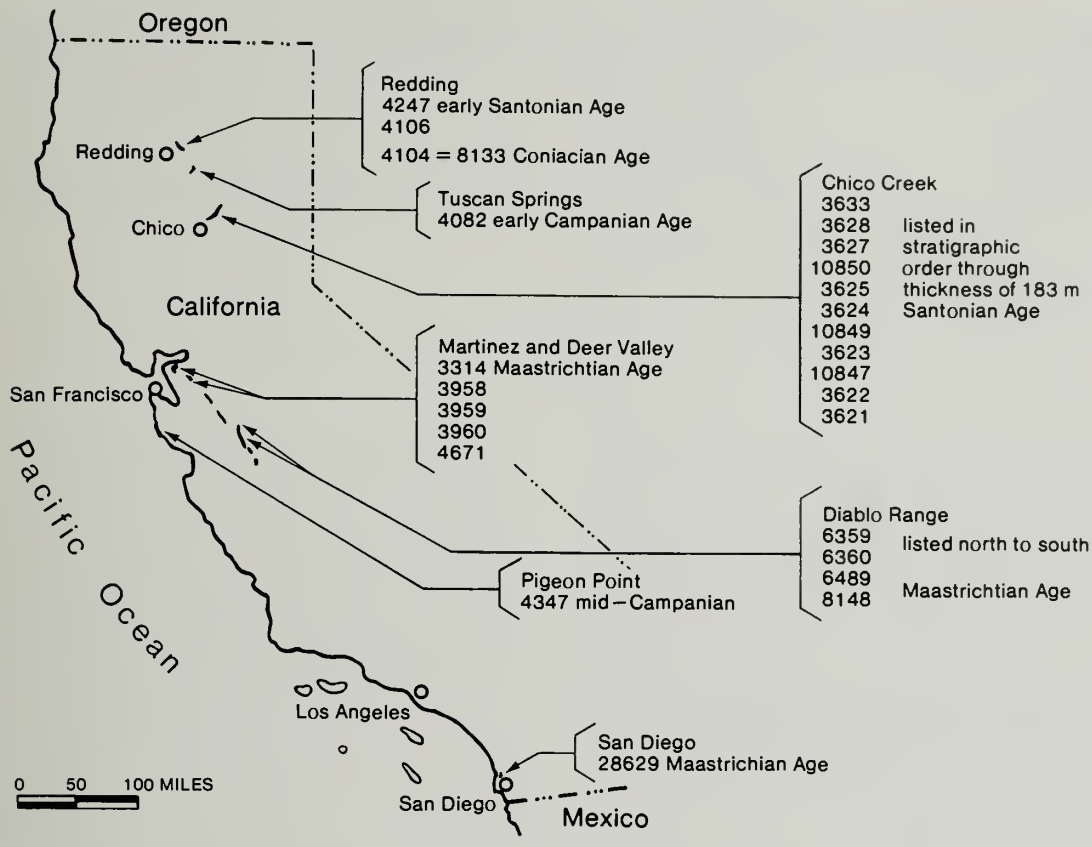


Figure 1

Index map to seven areas in California that have yielded donaciform bivalves of Late Cretaceous age. Localities listed for each area are described, or a reference to a description is given in Appendix 1—Localities Cited.

The hinge of the new genus ***Califadesma*** differs from that of *Mesodesma* Deshayes, 1832, in being less advanced but is indubitably that of a mesodesmatid. Unlike the hinge of *Mactropsis aequorea* (Conrad, 1833) (Figures 43, 44) with its resemblance to *Spisula,* the hinge of ***Califadesma*** is clearly homologous to those of Recent species of *Mesodesma,* such as *M. donacium* (Lamarck, 1818) (Figures 50, 51), *M. mactroides* Deshayes, 1855, and *M. (Ceronia) arctatum* (Conrad, 1830) (Figures 45, 46) and to those of the East Coast Miocene, *M. (C.) mariana* Glenn, 1904, and Pliocene, *M. (C.) spatha* Gardner, 1944. ***Califadesma*** is related to typical *Mesodesma* rather than to *Paphies* Lesson, 1831, which has smooth laterals and an austral distribution beginning as early as the early Miocene (Beu, 1971:117; Beu & De Rooij-Schuiling, 1982:212). ***Califadesma*** is thus the oldest known mesodesmatid.

Abbreviations used with locality and catalogue numbers are: ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences; CIT, California Institute of Technology; LACM, Natural History Museum of Los Angeles County, Malacology; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology; UCB, University of California, Berkeley; UCBMP, University of California, Berkeley, Museum of Paleontology; UCLA, University of California, Los Angeles.

DISTRIBUTION

The presence of both donacids and mesodesmatids in the California Upper Cretaceous is sporadic, and although specimens are abundant at some localities, they do not commonly constitute a major element of the faunas. They are abundant low in the Musty Buck Member of the Chico Formation on Chico Creek, Butte Co.; in a few beds of the Great Valley Series near Martinez and in Deer Valley, Contra Costa Co.; and in the Cabrillo Formation on Mt. Soladad, San Diego Co., California. They are locally common in the Redding Formation on the north side of Oak Run, Shasta Co., and in some beds of the Garzas Member of the Moreno Formation, Stanislaus Co., California. Donaciform bivalves, collected from localities in the seven areas indicated on Figure 1, have been studied for this report (see Appendix 1 for descriptions of localities). All of the mesodesmatids are from outcrops on the east side of the Sacramento Valley of northern California. Donacids occur with mesodesmatids in the northern California outcrops and additionally in central and southern California.

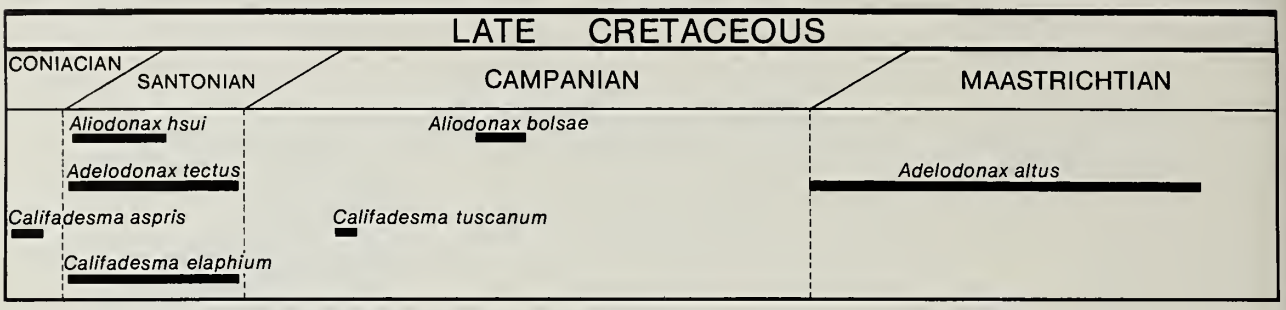


Figure 2

Geologic range chart for California Cretaceous species of Donacidae and Mesodesmatidae discussed in this paper.

The modern species of *Mesodesma* such as *M. donacium* of the Chilean coast and *M.* (*Ceronia*) *arctatum* of the northwest Atlantic coasts inhabit beaches to the south and north of the tropical to temperate donacids. Whether these Cretaceous records reflect a similar cooler water distribution for the mesodesmatids than for the donacids in the past or result from random preservation of sandy beach habitats is unclear.

Donacids are also longer ranging through the California Late Cretaceous than mesodesmatids. The presently known range of ***Califadesma*** is only from Coniacian through early Campanian, but that of the donacids is from Santonian into the late Maastrichtian. The geologic ranges of the species are shown in Figure 2.

Both *Notodonax*(***Aliodonax***) spp. and ***Califadesma*** spp. have relatively thick shells. An anteriorly compressed and posteriorly inflated shell, in several families, is an adaptation toward rapid burrowing (STANLEY, 1970), common among bivalves that frequently need reburying because they inhabit littoral substrates close to and within the surf zone. Rapid burrowers with thick shells (*Tivela, Mesodesma,* and *Donax*) occupy coarse, shifting substrate, where stability is essential (STANLEY, 1970:93).

Shells of ***Adelodonax*** spp. are of less than average thickness for donacids, and the paired valves have a more elongate, blade shape, which is efficient for rapid burrowing (STANLEY, 1970:59; VERMEIJ, 1987:312). Both sediment type and geologic occurrence agree with the morphologic implications of these clams and indicate that an abundance of either of these mesodesmatids or donacids is suggestive of a nearby shoreline.

Because the fossil record for such near-shore dwellers is relatively poor, VOKES (1945) expressed surprise at the number of Cretaceous donacid specimens that he was able to find. Most Cretaceous donacids have been described from the Atlantic basin; none of the species described from the Atlantic basin is closely related to the California species. California donacids resemble Maastrichtian species described from southern Argentina and Chile, and the mesodesmatids resemble typical late Cenozoic mesodesmatids of the Chilean coast. The lateral teeth of ***Califadesma*** are striate in the same manner as are those of *Mesodesma donacium* (Lamarck, 1818) (BEU & DE ROOIJ-SCHUILING, 1982:figs. 2b, c) and *M. mactroides* Deshayes, 1855, in that the dorsal sides of the laterals are more strongly striate than the ventral sides.

NARCHI (1981) indicated that paleontological records place the origin of the mesodesmatids in Australasia, but the geologically oldest is of Miocene age (BEU, 1971; BEU & DE ROOIJ-SCHUILING, 1982). *Mesodesma* is reported in the late Pliocene of Chile (HERM, 1969:94); it is inferred to have dispersed along the Patagonian coast during the Pleistocene, and *M. mactroides* to have only recently moved northward into Brazilian shores (NARCHI, 1981). The northern California specimens suggest a northern origin for the ancestors of typical *Mesodesma* and its north Atlantic subgenus *Ceronia* Gray, 1853.

Califadesma is first recognized in the Coniacian. Northern California Coniacian and Santonian faunas appear to reflect a cooler regime than do the earlier Turonian molluscan faunas or the later Campanian faunas (SAUL, 1986). ***Califadesma*** may have moved into northern California with the cooler water and left with the return of warmer water. ***Califadesma*** is a creditable ancestor for *Mesodesma,* despite the considerable time gap between the Late Cretaceous disappearance of ***Califadesma*** and the late Pliocene appearance of *Mesodesma.* The improbability that *Donacilla* (*Mesodesma*) *sakhalinensis* Kalishevich, 1967, from the late Eocene of Sakhalin can be included in *Mesodesma* is discussed under Mesodesmatidae. The Tertiary faunas of California are relatively well known and do not contain any *Mesodesma.* Their absence may reflect a paucity of sandy beach deposits. If ***Califadesma*** is ancestral to *Mesodesma,* the migration of this stock into southern waters might have been as early as Late Cretaceous but was not later than late Tertiary. The cool-water distribution of *Mesodesma* suggests that relatively cool periods during this time interval would have provided migration opportunities.

Donacids are unrecorded from Paleocene or between late Eocene and mid Pliocene in California, although another Recent sandy beach cohabiter, *Tivela,* is regularly represented in near-shore deposits beginning in the Oligocene. This lack of recorded donacids may result from the relatively small size of donacid shells and the uncom-

mon preservation of their sandy beach habitat which is usually sparsely fossiliferous when preserved and likely to be unexamined. Some ***Aliodonax*** shells preserve fine radial sculpture and structure, but none exhibits it to the extent usual among Holocene *Donax,* and none has denticulated valve margins. Possibly donacids were evolving the radial shell structure during the Late Cretaceous and Early Tertiary, but the absence of a better Early Tertiary record leaves the transition at present undocumented.

SYSTEMATIC PALEONTOLOGY

Order Veneroida H. & A. Adams, 1856

Superfamily Tellinacea de Blainville, 1814

Family Donacidae Fleming, 1828

Although donacids appeared later than tellinids, Pohlo (1967) suggested that the suspension-feeding donacids are unspecialized feeders and transitional to deposit-feeding tellinaceans. Donacids discussed in this paper have hinges with cardinal teeth that are not well separated from their lateral lamellae. These hinges are less advanced than those of tellinids of equivalent geologic age; thus, ancestors for tellinids must be sought elsewhere.

Genus *Notodonax* Feruglio, 1936

Type species by original designation *Donax annae-eugeniae* Feruglio, 1935.

The type species of *Notodonax* Feruglio, 1936, *Donax annae-eugeniae* from Patagonia, was described (Feruglio, 1935:90) from incomplete specimens interpreted to have two cardinals and an anterior lateral in each valve and two posterior laterals in the right valve and one in the left. The illustrations (Feruglio, 1936:pl 13, figs. 16–23) suggest that *Notodonax annae-eugeniae* bears considerable resemblance to *Notodonax* (***Aliodonax***) ***hsui*** sp. nov. and *N.* (*A.*) ***bolsae*** sp. nov. but has one more posterior lateral in each valve than is present in the California species. Additionally, the California species have one distinct cardinal in each valve, but the anterior cardinal is colaminal with the anterior lateral. Therefore the California species are placed in a new subgenus.

Aliodonax Saul, subgen. nov.

Type species *Notodonax* (***Aliodonax***) ***hsui*** Saul, sp. nov.

Diagnosis: ***Aliodonax*** is donaciform, solid, with a posterior angulation. Beaks are small, opisthogyral, and posterior to valve midline. Valve margin is smooth within. Ligament is in a deep groove behind short sturdy nymphs. Dentition consists of one posterior cardinal in each valve, 3b in right valve, 4b in left, and one posterior lateral in right valve. Anterior cardinals are not separated from anterior laterals, and in both valves the two form elongate colaminal anterior teeth, AIII-3a in right valve and AII-2 in the left. Right valve has long anterior "socket" into which thick and beveled anterior dorsal margin of left valve fits. Pallial sinus is short and rounded with dorsal arm sloping ventrally.

Discussion: The colaminal state of the anterior cardinals and laterals suggests a less evolved stage of hinge development than is described for *Notodonax s.s.* and *Protodonax* Vokes, 1945. Whereas in *Protodonax* the left valve hinge formula is AII 2 4b PII, in ***Aliodonax*** it is AII-2 4b (see Figure 3 for hinge diagrams and formulae). No complete right-valve hinge of *Protodonax* has been described. The two California species comprising ***Aliodonax*** have fewer and shorter laterals (especially posterior laterals), and a larger, more robust nymph than do species of *Protodonax.* Vokes (1945) did not find radial sculpture in *Protodonax* species nor is its presence mentioned by Feruglio (1936) in describing *Notodonax.* Fine radial sculpture and structure is present in the surficial shell layer of the posterior quarter of valves of *N.* (*A.*) ***hsui.*** It has not been recognized in valves of *N.* (*A.*) ***bolsae***, but the shells of *N.* (*A.*) ***bolsae*** are so completely recrystallized that such structure and sculpture might have been obliterated. Radial structure is present in a medial shell layer of Holocene donacids from the eastern Pacific Panamic province (Keen, 1971:234).

The name ***Aliodonax*** is compounded of the Latin *alius* meaning "another" or "other," and *Donax,* a bivalve genus. *Donax* is of masculine gender.

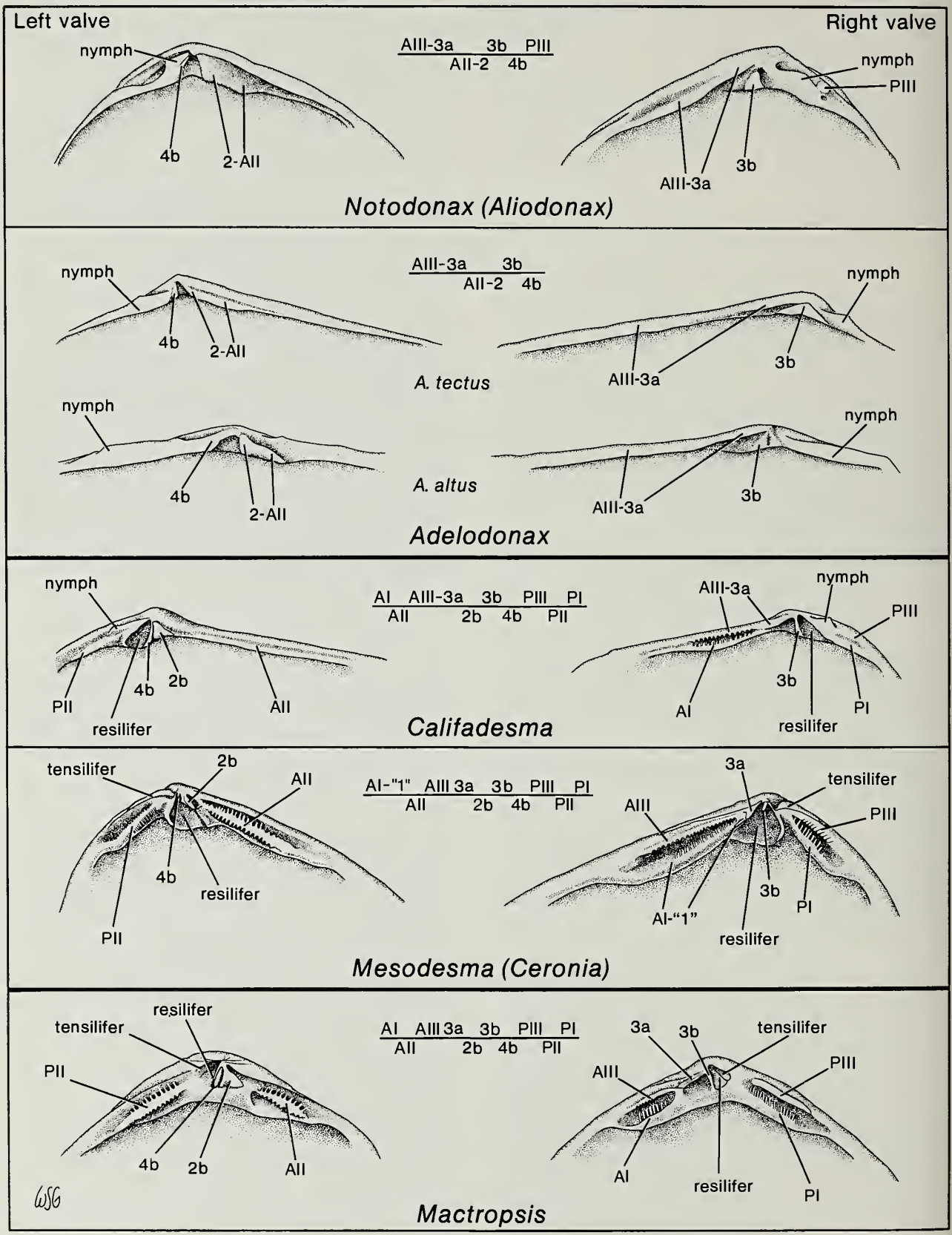
Notodonax (***Aliodonax***) ***hsui*** Saul, sp. nov.

(Figures 4–14)

Diagnosis: Elongate ***Aliodonax*** having the beak within the posterior third of the shell length. The hinge has, in the right valve aligned with the anterior hinge plate and valve margins, a long anterior colaminal tooth that is low adjacent to the beak and becomes high distally.

Description: Shell large for a donacid, thick. Valves elongate, compressed anteriorly, inflated and truncated posteriorly; anterodorsal margin nearly straight; anterior margin rounded, curving smoothly into ventral margin; ventral margin barely convex, angled abruptly into posterior margin; posterior margin nearly at right angle to ventral, rather straight, curving into very short posterodorsal margin; posterior angulation abrupt, parallel to and very near posterior margin. Beaks small, opisthogyral, very near posterior end; umbonal area blunt and broad. Lunule long, slightly depressed, bounded by low angulation. Exterior of valves with unevenly prominent growth lines and obscure radial ribbing on posterior quarter of shell.

Hinge with heavy, short nymph and deep ligament groove. Hinge of right valve with large, deltoid 3b vertically directed, immediately under beak; colaminal 3a-AIII very long, low and at valve margin dorsally, becoming high, bladelike, and aligned with hinge plate margin; long anterior "socket" for left valve anterior margin, dorsal to 3a-AIII; posterior lateral a low node just at base of ligament


Left valve
Right valve
nymph
AIII-3a 3b PIII
AII-2 4b
4b
2-AII
nymph
PIII
3b
AIII-3a
Notodonax (Aliodonax)
nymph
AIII-3a 3b
AII-2 4b
4b
2-AII
nymph
3b
AIII-3a
A. tectus
nymph
4b
2-AII
nymph
AIII-3a
3b
A. altus
Adelodonax
nymph
AI AIII-3a 3b PIII PI
AII 2b 4b PII
PII
4b
2b
AII
resilifer
AIII-3a
nymph
PIII
3b
AI
PI
resilifer
Califadesma
tensilifer
2b
AII
AI-"1" AIII 3a 3b PIII PI
AII 2b 4b PII
4b
resilifer
PII
3a
tensilifer
AIII
PIII
3b
PI
AI-"1"
resilifer
Mesodesma (Ceronia)
resilifer
tensilifer
PII
AI AIII 3a 3b PIII PI
AII 2b 4b PII
4b
2b
AII
3a
3b
tensilifer
AIII
PIII
AI
resilifer
PI
WSG
Mactropsis

groove. Pallial sinus extending just beyond line dropped from beaks, rounded; dorsal arm sloping ventrally from posterior adductor muscle scar; ventral arm partially confluent with pallial line. Muscle scars nearly equal, rather round; anterior scar distant from beaks; posterior scar very near beaks. Interior valve margin smooth.

Holotype: LACMIP 7813.

Paratypes: LACMIP 7814 from CIT loc. 1016, Chico Creek; 7861 from UCLA loc. 3621, Chico Creek; 7815–7817 from UCLA loc. 3622, Chico Creek; 7818 from UCLA loc. 3628, Chico Creek, Paradise Quadrangle, Butte Co.; 7819 from UCLA loc. 4247, south side of Oak Run, Millville Quadrangle, Shasta Co., California.

Dimensions: Of holotype, length 54 mm, height 30.5 mm, inflation of single valve 11 mm, length beak to posterior 12 mm; of paratype LACMIP 7815, length 24 mm, height 12 mm, inflation of single valve 4.4 mm, length beak to posterior 8.3 mm; of paratype LACMIP 7816, length 21.4 mm, height 9 mm, inflation of single valve 3.4 mm, length beak to posterior 6.3 mm; of paratype LACMIP 7819, length 21.9 mm, height 11.1 mm, inflation of single valve 4.3 mm, length beak to posterior 6.8 mm.

Type locality: UCLA loc. 3621, Chico Creek, Paradise Quadrangle, Butte Co., California.

Distribution: Musty Buck Member of the Chico Formation, from 370 to 450 m above the base of the section on Chico Creek (UCLA locs. 3621, 3622, 3625, CIT loc. 1016), Butte Co.; Redding Formation on south side of Oak Run (UCLA loc. 4247), Millville Quadrangle, Shasta Co., California.

Age: Santonian.

Remarks: The holotype is a large right valve. Large valves are strongly truncate posteriorly, but the growth lines indicate that the shape changes ontogenetically, and small valves are less truncate posteriorly and relatively less produced anteriorly. The pallial sinus is described from one of these small individuals. No left valve is available. Small individuals resemble both ***Califadesma elaphium*** sp. nov. and ***Adelodonax tectus*** sp. nov. with which they co-occur. Anterodorsal and ventral margins of *Notodonax* (*A.*) ***hsui*** slope toward each other, and the valves wedge anteriorly more than do those of ***Califadesma elaphium***; *N.* (*A.*) ***hsui*** lacks the double posterior angulation of ***C. elaphium***. *Notodonax* (*A.*) ***hsui*** differs from the similarly shaped ***A. tectus*** in having better developed hinge teeth, a shorter nymph, the ventral arm of the pallial sinus partially confluent with the pallial line, and radial riblets (Figure 7) on the posterior quarter of the valve.

The species is named for K. J. Hsu who assisted in measuring the Chico Creek section.

Notodonax (***Aliodonax***) ***bolsae*** Saul, sp. nov.

(Figures 16–21)

Diagnosis: Moderately elongate ***Aliodonax*** having beak more than a third of the shell length from the posterior margin. Hinge of right valve has a long anterior colaminal tooth, at an angle to the hinge plate and valve margins, that is relatively high adjacent to the beak.

Description: Shell large for a donacid; valves elongate, compressed anteriorly, inflated and truncated posteriorly; anterodorsal margin nearly straight; anterior margin rounded, curving smoothly into ventral margin; ventral margin broadly convex, angled abruptly into posterior margin; posterior margin at about 60° to ventral, rather straight, curving into very short posterodorsal margin; posterior angulation strong, parallel to and very near posterior margin. Beaks small, opisthogyral, near posterior third; umbonal area blunt and broad. Exterior of valves with unevenly prominent growth lines.

Hinge with heavy, short nymphs and deep ligament groove. Hinge of right valve with large, anteriorly slanted, deltoid 3b and long, thin, colaminal 3a-AIII; long, well developed anterior "socket" for margin of left valve; posterior lateral a low node just behind base of ligament groove. Hinge of left valve with posteriorly hooked, anteriorly directed, elongate 2-AII and short, lamellar, posteriorly directed 4b. Pallial sinus and muscle scars unknown. Interior valve margin smooth.

Holotype: LACMIP 7820.

Paratypes: LACMIP 7821–7824 from UCLA loc. 4347, near Bolsa Point, Pigeon Point Quadrangle, San Mateo Co., California.

Dimensions: Of holotype, somewhat crushed posteriorly, length 44.4 mm, height 27.5 mm, thickness 10 mm, distance of beak from posterior 14.3 mm; of paratype LACMIP 7821, length 37.4 mm, height 20.5 mm, thickness 6.4 mm, distance of beak from posterior 14.3 mm.

Type locality: UCLA loc. 4347, about 880 m north of

←

Figure 3

Diagrams of hinges and hinge formulae of supraspecific donacid and mesodesmatid taxa discussed in this paper. All hinges enlarged to approximately equal size. Both ***Aliodonax*** and ***Adelodonax*** have lucinoid-type hinges. These hinges are primitive in that cardinal tooth 2 is attached to lateral AII and cardinal 3a is attached to lateral AIII. ***Califadesma*** and *Mesodesma* have arcticoid-type hinges that are strongly modified by the submergence of the resilium and in *Mesodesma* by its forward rotation. In ***Califadesma*** the cardinal teeth, although crowded forward, are readily recognizable, but in *Mesodesma* the cardinals are vestigial and not easily seen without some magnification.

Bolsa Point, Pigeon Point Quadrangle, San Mateo Co., California.

Distribution: Known only from the type locality.

Age: Campanian.

Remarks: All five specimens of *Notodonax* (*A.*) ***bolsae*** are tectonically somewhat distorted and the shell material is recrystallized. *Notodonax* (*A.*) ***bolsae*** has a longer more sloping posterodorsal margin resulting in beaks that are more centrally positioned than in *N.* ***hsui.***

The species is named for its occurrence at Bolsa Point, San Mateo Co., California.

Genus *Adelodonax* Saul, gen. nov.

Type species *Adelodonax tectus* Saul, sp. nov.

Diagnosis: Valves of ***Adelodonax*** are smooth except for growth lines, elongate, and moderately inflated. Low beaks are slightly opisthogyral and posterior to the middle. Ligament is behind a long nymph. Hinge of right valve has one triangular cardinal (3b); a socket anterior to the cardinal, and an elongate, colaminal anterior tooth (AIII-3a). Left valve has one elongate, colaminal anterior tooth (AII-2) ventral to a long socket, a shallow socket beneath beak, and usually a low cardinal (4b) posterior to the shallow socket. Anterior adductor muscle scar is well impressed for such a thin shell and subtriangular in shape; posterior adductor muscle scar is plumply ovoid in shape. Pallial sinus is of moderate depth. U-shaped, and distant from pallial line.

Discussion: ***Adelodonax*** is doubtfully placed in the family Donacidae. The hinge teeth are delicate and difficult to expose from the matrix. They are reminiscent of juvenile hinges or an early stage in the development of the lucinoid hinge. In their indistinctness they resemble those of Quenstedtiidae Cox, 1929b; ***Adelodonax,*** however, has a ligament groove behind an alate nymph but does not have a ligament pit. The hinge teeth are somewhat better defined than those of Quenstedtiidae and might be derived therefrom, but to evolve a ligament seated in a groove behind an alate nymph from a ligament in a pit requires considerable change both to the shell attachment area and the structure of the ligament. ***Adelodonax*** has anterior laterals but not the long anterior and posterior laterals of Sowerbyiidae Cox, 1929b; anterior laterals are usually absent in Tancrediidae Meek, 1864 (Cox, 1929a). The nymph and ligament groove of ***Adelodonax*** are long for a donacid. The dorsal ends of the long colaminal teeth have not yet differentiated into cardinals, and ***Adelodonax*** differs from other Donacidae in having one rather than two cardinals in each valve and in lacking posterior laterals (see Figure 3 for hinge diagrams and formulae). The valves may gape slightly posteriorly.

Cox (1929a) and Chavan (1950) suggested that Donacidae are derived from Tancrediidae. Three supraspecific tancrediid taxa—*Palaeomya* Zittel & Goubert, 1861, *Isotancredia* Chavan, 1950, and *Paratancredia* Chavan, 1950—resemble ***Adelodonax*** in shape, but differ from ***Adelodonax*** in having posterior laterals and lacking a pallial sinus. Both *Isotancredia* and *Paratancredia* resemble ***Adelodonax*** in having an anterior colaminal tooth (AIII-3a) in the right valve. *Eodonax* Cox, 1929a, and *Protodonax* possess characteristics considered to be intermediate between the two families (Cox, 1929a; Vokes, 1945; Chavan, 1950) and the classification of each has oscillated between both families. ***Adelodonax*** also has characteristics that may be intermediate. The anterior colaminal teeth are suggestive of Tancrediidae, but an absence of posterior laterals suggests Donacidae. The hinge is more primitive than that of any other donacid and more primitive than that of most Tancrediidae, but the pallial sinus is deeper than that of tancrediids and suggests Donacidae.

Adelodonax bears a strong resemblance to *Ceroniola* Wilckens, 1904. Keen (*in* Moore, 1969:N609) follows Wilckens (1904) in considering this small, thin bivalve to be related to *Mesodesma,* and Stinnesbeck (1986) has reaffirmed this classification. The left valve hinge of ***Adelodonax*** differs from that of *Ceroniola* in lacking posterior laterals; in ***Adelodonax*** the depression between AII-2 and 4b is here interpreted as a socket for 3b; whereas, for *Ceroniola,* Keen (*in* Moore, 1969) and Stinnesbeck (1986) have interpreted this as a resilifer. The most prominent tooth in the right valve hinge of ***Adelodonax,*** cardinal 3b, is shaped and positioned to fit this socket. Illustrations of *Ceroniola* suggest that this area beneath the beak is the damaged portion of the right valve; if so, a resilifer has not been clearly demonstrated to be present in *Ceroniola,* and it and ***Adelodonax*** may be confamilial.

Adelodonax also resembles *Amphichaena* Philippi, 1847, in shape but the hinge teeth of *Amphichaena* are concentrated closer to the beaks, and the hinge is more advanced with a hinge formula of AI-3a 3b in the right valve and AII-2 4b in the left valve.

The name ***Adelodonax*** is compounded from the Greek *adelos,* meaning "unseen, unknown, obscure," and *Donax,* a bivalve genus of masculine gender.

Adelodonax tectus Saul, sp. nov.

(Figures 14, 22–28)

Diagnosis: ***Adelodonax*** having the beak very near the posterior end and a moderate posterior angulation.

Description: Shell thin, small; valves elongate, compressed and produced anteriorly, moderately inflated and truncated posteriorly; anterodorsal margin rather straight, anterior margin bluntly rounded, ventral margin barely convex, posterior margin truncated. Beaks opisthogyral, situated very near posterior end. Lunule depressed, long

Explanation of Figures 4 to 21

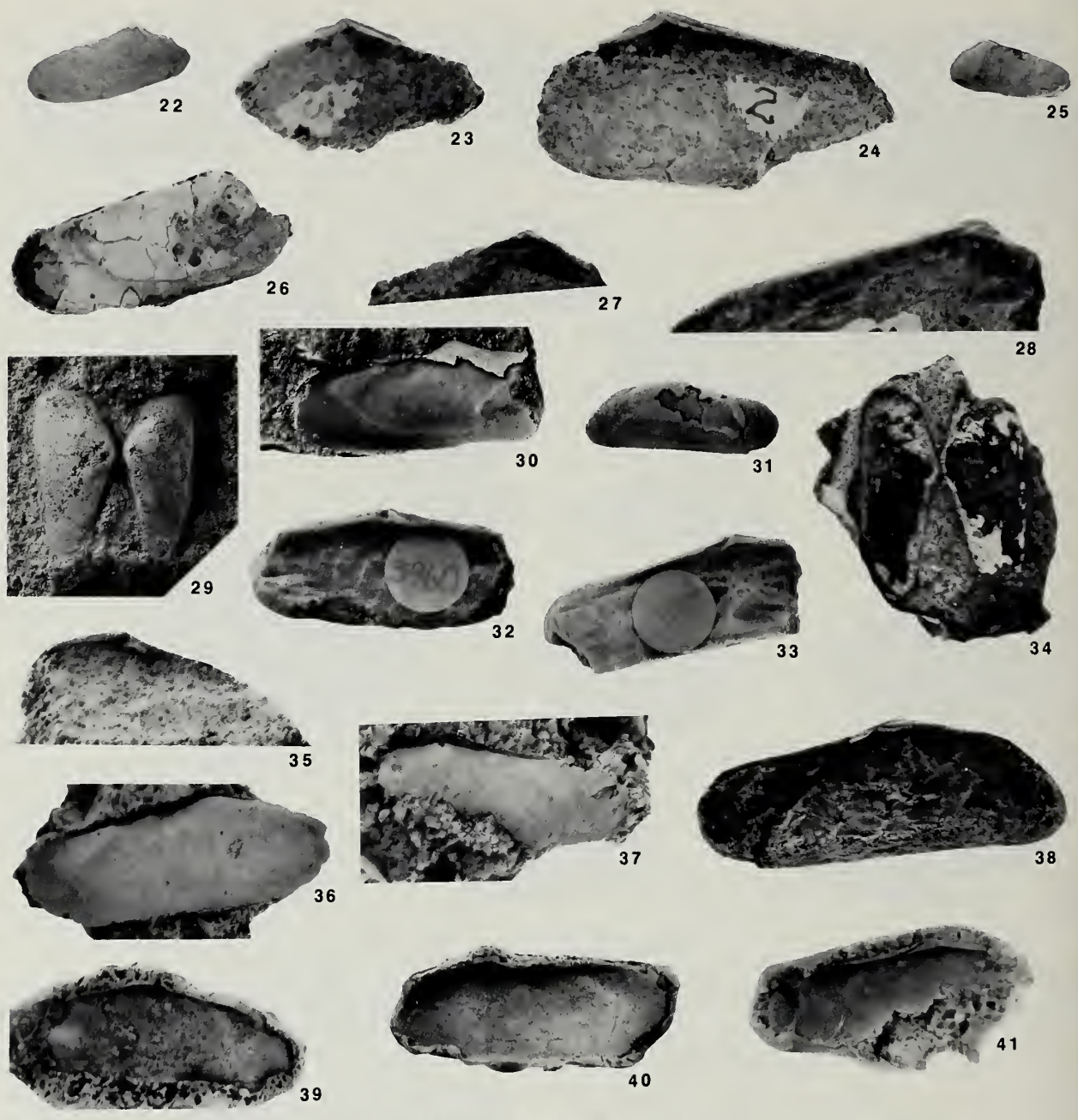
Figures 4–13. *Notodonax* (***Aliodonax***) ***hsui*** sp. nov., right valve. Figure 4: LACMIP 7813 from UCLA loc. 3621, holotype, ×1. Figures 5–7: LACMIP 7819 from UCLA loc. 4247, paratype, ×2; Figure 5, hinge, teeth worn; Figure 6, posterior; Figure 7, fine radial ribbing on dorsal half. Figures 8, 9: LACMIP 7814 from CIT loc. 1014, paratype, ×1; Figure 8, hinge, nymph chipped; Figure 9, exterior. Figures 10, 11: LACMIP 7815 from UCLA loc. 3622, paratype; Figure 10, exterior, ×1.5; Figure 11, hinge, ×2. Figure 12: LACMIP 7816 from UCLA loc. 3622, paratype, ×1.5. Figure 13: LACMIP 7818 from UCLA loc. 3628, paratype, ×1.5.

Figures 14, 15. Two sides of sandstone fragment Chico Formation, Musty Buck Member, UCLA loc. 3622, ×1. Figure 14: *Notodonax* (***Aliodonax***) ***hsui***, LACMIP 7817, and ***Adelodonax tectus*** sp. nov., LACMIP 7832. Figure 15: ***Califadesma elaphium*** sp. nov., LACMIP 7853.

Figures 16–21. *Notodonax* (***Aliodonax***) ***bolsae*** sp. nov., from UCLA loc. 4347. Figures 16, 17: LACMIP 7822, paratype, left valve, ×1; Figure 16, hinge; Figure 17, exterior. Figures 18, 21: LACMIP 7820, holotype, right valve slightly crushed posteriorly, ×1; Figure 18, hinge, nymph chipped; Figure 21, exterior. Figures 19, 20: LACMIP 7821, paratype, left valve, distorted longitudinally, ×1; Figure 19, hinge; Figure 20, exterior.

and very narrow; posterior angulation low. Exterior of valves polished, showing only growth lines.

Hinge with prominent nymph for ligament. Right valve with triangular, low rounded 3b with indistinct socket posterior to it and better defined socket anterior to it; colaminal AIII-3a very long, lamellar, extending from immediately in front of beak for nearly one-third length of anterodorsal margin. Left valve with elongate colaminal AII-2 and short obscure cardinal 4b on either side of the triangular, shallow, round-bottomed socket for 3b. Pallial line distant from valve margin anteriorly, becoming moderately close to margin posteriorly; pallial sinus U-shaped,



Explanation of Figures 22 to 41

Figures 22–28. ***Adelodonax tectus*** sp. nov., from UCLA 3622. Figure 22: LACMIP 7825, holotype, left valve, ×1. Figure 23: LACMIP 7827, paratype, hinge left valve, ×3. Figure 24: LACMIP 7826, paratype, hinge left valve, ×3. Figure 25: LACMIP 7829, paratype, right valve, ×1. Figure 26: LACMIP 7828, paratype, right valve, pallial sinus, ×2. Figure 27: LACMIP 7830, paratype, hinge right valve, ×2. Figure 28: LACMIP 7831, paratype, hinge right valve, ×3.

Figures 29–41. ***Adelodonax altus*** (Gabb, 1864). Figure 29: ANSP 4557 from Martinez, Contra Costa Co., Calif., lectotype, ×2. Photo by Takeo Susuki. Figure 30: ANSP 71880 from Martinez, Contra Costa Co., Calif., paralectotype, left valve showing trace of pallial line, ×2. Photo by Takeo Susuki. Figures 31, 38: LACMIP 7843 from UCLA 6489, hypotype, right valve; Figure 31, exterior, ×1; Figure 38, hinge, ×2. Figure 32: LACMIP 7841 from UCLA 3960, hypotype, hinge left valve, ×2. Figure 33: LACMIP 7840 from UCLA loc. 3958, hypotype, hinge right valve, ×2. Figure 34: LACMIP 7842 from UCLA loc. 3960, hypotype, "butterflied" valves, ×1.5. Figure 35: LACMIP 7862 from UCLA loc. 6489, hypotype, hinge left valve, ×2. Figures 36, 40: LACMIP 7837 from LACMIP 28629, hypotype, interior left valve, ×2; Figure 36, rock mold; Figure 40, latex pull. Figures 37, 41: LACMIP 7839 from LACMIP loc. 28629, hypotype, hinge right valve, ×2; Figure 37, rock mold; Figure 41, latex pull. Figure 39: LACMIP 7838 from LACMIP loc. 28629, hypotype, interior of left valve, latex pull, ×2.

horizontal, extending to point just anterior to beaks. Muscle scars nearly equal, round, usually well impressed, posterior scar very near beaks, anterior scar distant.

Holotype: LACMIP 7825.

Paratypes: LACMIP 7826–7835 from UCLA loc. 3622 and LACMIP 7836 from UCLA loc. 3623.

Dimensions: LACMIP 7825, length 25 mm, height 10 mm, inflation of single valve 3.7 mm, beak to posterior 7 mm; LACMIP 7829, right valve length 18 mm, height 7.8 mm, inflation of single valve 2 mm, beak to posterior 6 mm.

Type locality: UCLA loc. 3622, Chico Creek, Paradise Quadrangle, Butte Co., California.

Distribution: 440 m (1320 feet) to 560 m (1740 feet) above the base of the Chico Creek section in the Musty Buck Member of the Chico Formation (UCLA locs. 3622–3624, 3627, 3633), Butte Co., California.

Age: Santonian.

Remarks: ***Adelodonax tectus*** has the beaks more posteriorly placed, and the valves shorter than those of ***A. altus***. ***Adelodonax tectus*** is less elongate than *Ceroniola australis* and has a relatively longer nymph.

At its type locality on Chico Creek, ***Adelodonax tectus*** occurs in abundance with *Notodonax* (***Aliodonax***) ***hsui*** and ***Califadesma elaphium***; all three are of similar shape. Large specimens of *N.* (***A.***) ***hsui*** are readily distinguished from ***A. tectus*** by their abrupt posterior angulation, but small individuals have a less abrupt angulation. They can be distinguished from ***A. tectus*** by their better developed hinge teeth, presence of radial striations on the posterior quarter of the shell, and broader pallial sinus, the lower limb of which is partially confluent with the pallial line. ***Califadesma elaphium*** is most readily distinguished from ***Adelodonax tectus*** by the double angulation of the posterior slope on the former.

The specific name is from the Greek *tecktos,* meaning "soluble," and refers to the leached condition of most specimens from the type locality.

Adelodonax altus (Gabb, 1864)

(Figures 29–41)

Pharella alta Gabb, 1864:147, pl. 22, fig. 118; Stewart, 1930: 293, pl. 5, fig. 11.

Diagnosis: Elongate ***Adelodonax*** with the beak at the posterior third and having a slight posterior truncation.

Description: Shell thin, small; valves elongate, compressed and produced anteriorly, moderately inflated and slightly truncated posteriorly; anterodorsal margin rather straight, anterior margin bluntly rounded, ventral margin nearly straight, posterior margin truncated. Beaks opisthogyral, situated at posterior third of the valve. Lunule depressed, long and very narrow; posterior angulation very low. Exterior of valves polished, showing only growth lines.

Hinge with prominent nymph for ligament. Right valve with triangular, low rounded 3b with indistinct socket posterior to it and better defined socket anterior to it; colaminal AIII-3a very long, lamellar, extending from immediately in front of beak for nearly one-third length of anterodorsal margin. Left valve with AII-2 long, lamellar, and extending anterior to long lateral socket; 4b a slightly raised welt on hinge plate posterior to triangular, shallow, round-bottomed socket. Pallial line distant from valve margin anteriorly, becoming moderately close to margin posteriorly; pallial sinus U-shaped, horizontal, extending to point just anterior to beaks. Muscle scars of nearly equal size; posterior scar very near beaks; anterior scar distant, moderately well impressed, acutely subtrigonal.

Lectotype: ANSP 4557, **herein designated**. Stewart (1930:293) could not recognize the specimen figured by Gabb (1864). He suggested that if no better specimen from Gabb's original material was found, the specimen Stewart (1930:pl. 5, fig. 11) figured might be designated lectotype. That specimen has been missing since 1960 (Elana Benamy, *in litt.*, 20 Nov. 1987). Two specimens remain of Gabb's original material: an incomplete left valve similar in size to the specimen figured by Stewart and a "butterflied" pair of valves that are one-third smaller. The "butterflied" pair of valves, although small, provides a better indication of valve shape and is chosen as lectotype (Figure 29).

Paralectotype: ANSP 71880 (Figure 30).

Hypotypes: LACMIP 7837–7839 from LACMIP loc. 28629, LACMIP 7840 from UCLA loc. 3958, LACMIP 7841–7842 from UCLA loc. 3960, LACMIP 7843 from UCLA 6489.

Dimensions: Lectotype ANSP 4557 right valve, length 12 mm, height 6.5 mm, beak to posterior 4.8 mm; hypotype LACMIP 7842, length 14 mm, height 6.4 mm, beak to posterior 5.8 mm.

Type locality: Near Martinez, Contra Costa Co., California (Gabb, 1864).

Distribution: Great Valley Series near Martinez and Deer Valley, Contra Costa Co.; Garzas Member of the Moreno Formation near Garzas (LACMIP loc. 8148) and Orestimba creeks (UCLA locs. 6359, 6360, 6489), Merced and Stanislaus cos., California. Poorly preserved specimens from the Cabrillo Formation on Mt. Soledad (LACMIP loc. 28629), San Diego Co. (identified as "*Pharella alta*" in Kennedy, 1975:15). Rosario Formation on the north side of Punta Banda (UCLA loc. 7137), Baja California, Mexico.

Age: Maastrichtian. Gabb (1864) indicated that *Pharella alta* was from the "Martinez Group," but it has not subsequently been recovered from deposits of Paleocene age near Martinez. Stewart (1930:293) recognized that

the rock type and preservation are typical of the Late Cretaceous Great Valley Series from the vicinity of Martinez, Contra Costa Co., California, and at several Contra Costa County localities (UCLA locs. 3958, 3959, 3960, 3314, and 4671), it has been found in association with species indicative of late Maastrichtian age. The Cabrillo Formation on Mt. Soledad, which yields abundant ***Adelodonax altus,*** is not continuous with other outcrops of the Cabrillo Formation (KENNEDY, 1975), and no other age diagnostic fossils have been found there. The specimen from the Rosario Formation on Punta Banda, Baja California, occurs with other mollusks of early Maastrichtian age.

Remarks: STEWART (1930:293) suspected that this species was not a *Pharella,* but did not reassign it. He mistook the anterior for the posterior, indicating that the shell is "produced posteriorly" and that the beaks are prosogyral and anterior to the valve middle. The position of the pallial sinus shows "*Pharella*" *alta* Gabb, 1864, to be anteriorly produced.

Although GABB (1864) did not mention any similarity between *Pharella alta* and *Cultellus australis* Gabb, 1860, described from Chile, the two are similar in shape. *Cultellus australis* has a somewhat more anteriorly elongate shell than *P. alta.* The Chilean species was moved to *Solen*[?] (*Cultellus*) by PHILIPPI (1887), and designated the type species of the new genus *Ceroniola* by WILCKENS (1904: 249, pl. XX, figs. 11a, b, 12, 13). The left hinge of *Ceroniola australis* (Gabb, 1860) (WILCKENS, 1904:pl. XX, fig. 11a; STINNESBECK, 1986: pl. 4, fig. 3) resembles that of ***Adelodonax altus*** except for the presence of posterior laterals in the former. WILCKENS (1904) lacked a complete right valve hinge of *Ceroniola australis,* and STINNESBECK's right valve is also incomplete (1986:pl. 4, fig. 4). STINNESBECK appears to have inadvertently flipped the negatives so that the right and left hinges of *Ceroniola australis* are printed as mirror images (1986:pl. 4, figs. 3, 4). WILCKENS (1904: 249, pl. XX, fig. 13) described a long anterior and a short posterior groove. He considered the posterior groove to be too distant from the valve margin to be a ligament groove. The common preservation of specimens of ***Adelodonax*** in the butterfly position with the nymphs adjacent suggests that the ligament attached the valves here and that the similar groove and nymph structure of *Ceroniola* may have been the site of ligament attachment. The age of *Ceroniola australis* (Gabb), which is from the Quiriquina Formation (WILCKENS, 1904:205; STINNESBECK, 1986) is erroneously given as "U. Tertiary" by Keen (*in* MOORE, 1969:N609). PHILIPPI (1887) referred the Quiriquina beds to the Unter Tertiaren, but the Quiriquina beds were regarded as Cretaceous by WILCKENS (1904) and are presently considered to be of Maastrichtian age (STINNESBECK, 1986; RICCARDI, 1987:table III). Thus the type species, *Ceroniola australis* is from the same stage as ***Adelodonax*** *altus* (Gabb).

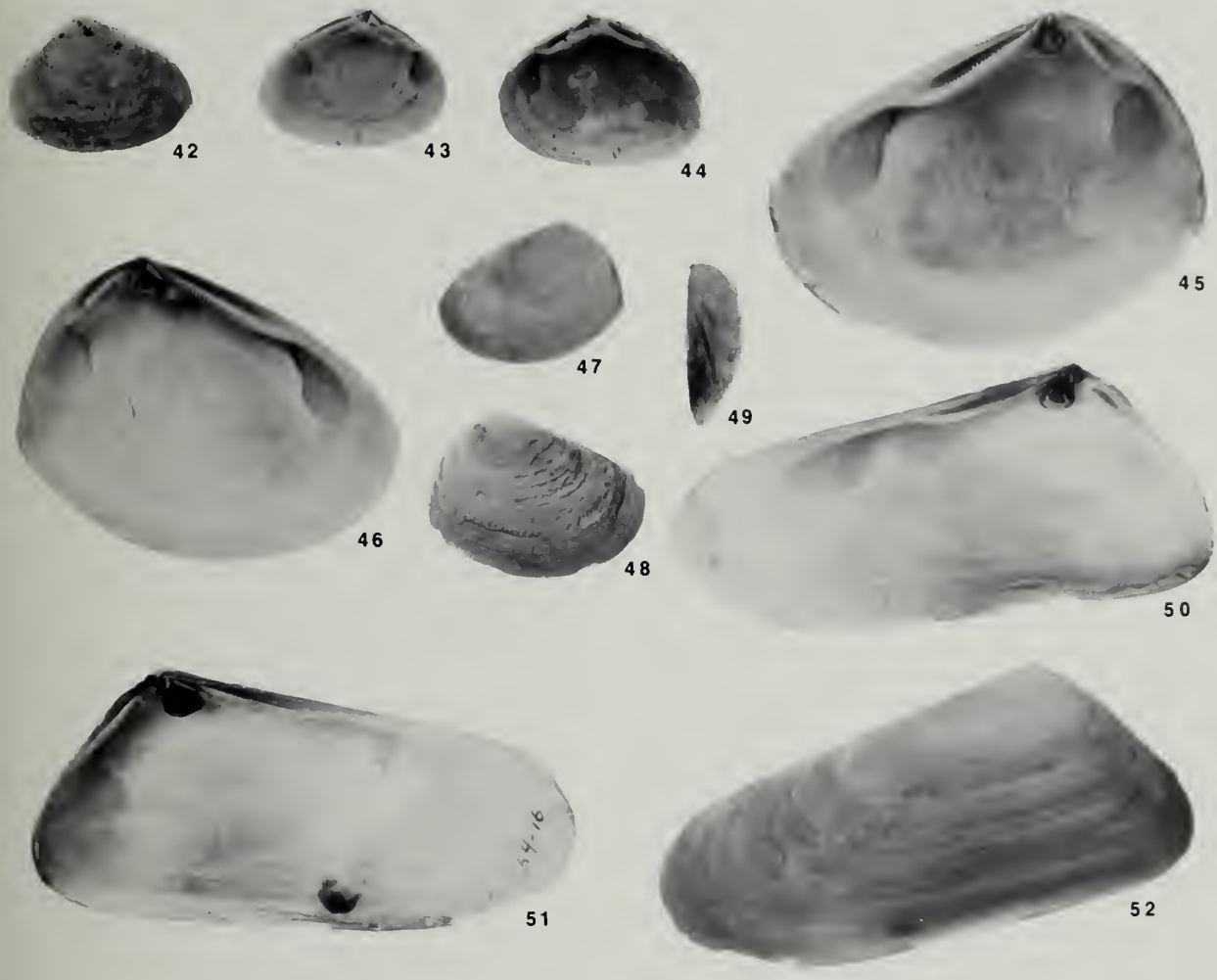
Specimens of ***Adelodonax*** *altus* are usually poorly preserved, in part because the shells are thin and in part because the sandstone matrix in which they occur is porous and subjects them to leaching. The best specimens are from the Great Valley Series near Martinez and Deer Valley, Contra Costa Co. The specimens from the Cabrillo Formation on Mt. Soledad, San Diego Co., are mainly molds in a coarse, mica-rich sandstone matrix. Despite the coarse-grained matrix, latex pulls provide hinge details (Figures 36, 37, 39–41). Well preserved specimens are also present in hard sandstone of the Rosario Formation on the north side of Punta Banda, Baja California, Mexico (UCLA loc. 7137), associated with a diverse bivalve and gastropod fauna (SAUL, 1970) that is probably of early Maastrichtian age.

Superfamily MACTRACEA Lamarck, 1809

DALL (1898:910) placed the genus *Mactropsis* Conrad, 1854, in the Mesodesmatidae, apparently because of its thick shell, as he stated (1898:907–908) that fossil species of Mesodesmatidae might be distinguished from the mactrids by their excessive solidity and thickness of their valves rather than by any clearly marked differential characters. He did not, however, exclude certain other thick shelled forms from the Mactridae, *e.g., Pseudocardium* Gabb, 1866. Keen (*in* MOORE, 1969:N610) and BEU (1971) retained *Mactropsis* in the Mesodesmatidae, but PALMER & BRANN (1965:190) included it in the Mactridae, a placement with which I concur.

DALL (1895:910–911) considered *Mactropsis* an ancestral mesodesmatid, and he stressed the more primitive features of its hinge with respect to the hinge of Recent *Mesodesma.* In addition to the features described by Dall, *Mactropsis* has left valve laterals AII and PII that are strongly striated on both sides and right valve laterals that are strongly striated on one face, AI and PI on their dorsal face and AIII and PIII on their ventral face. These laterals resemble those of *Spisula.* Anterior lateral AI is not bimodal and shows no inclination toward the formation of an incipient cardinal 1 (Figure 3). The tensilifer and resilifer, which are not separated by a shelly partition, are of equal length, but the resilifer is approximately three times as wide as the tensilifer. The tensilifer is on the inner slope of the valve margin but exteriorly exposed in a narrow wedge just behind the beak. Figures 43 and 44 are of the hinge of the type species of *Mactropsis, Erycina aequorea* Conrad, 1833 (by subsequent designation, DALL, 1895).

In Recent species of *Mesodesma* the tensilifer is in a more external position than is that of *Mactropsis.* The tensilifer of *Mesodesma donacium* is a wide-based triangle with the dorsal side external and the anterior side internal and set off from the resilifer by the steeply depressed posterior side of the resilifer (Figures 50, 51). In *Mesodesma* (*Ceronia*) *arctatum* the tensilifer is smaller relative to the resilifer and set off from the resilifer by the overhanging edge of the deeply depressed posterior side of the resilifer (Figures 45, 46). In addition, *Mesodesma donacium* has



Explanation of Figures 42 to 52

Figures 42–44. *Mactropsis aequorea* (Conrad, 1833) from LACMIP loc. 5659, hypotypes. Figures 42, 43: LACMIP 7860, left valve, ×2; Figure 42, exterior; Figure 43, interior (see Figure 3 for labeling of teeth). Figure 44: LACMIP 7859, interior right valve, ×3 (see Figure 3 for labeling of teeth).

Figures 45–49. *Mesodesma* (*Ceronia*) *arctatum* (Conrad, 1830) from Hampton Harbor, New Hampshire, hypotypes. Figures 45, 48, 49: LACM 104120, right valve; Figure 45, interior, ×2 (see Figure 3 for labeling of teeth); Figure 48, exterior, ×1; Figure 49, posterior, ×1. Figures 46, 47: LACM 104121, left valve; Figure 46, interior, ×2 (see Figure 3 for labeling of teeth); Figure 47, exterior, ×1.

Figures 50–52. *Mesodesma donacium* (Lamarck, 1818) from Iquique, Chile, hypotypes, ×1. Figure 50: LACM 64-16.1, right valve interior (see Figure 3 for labeling of teeth). Figures 51, 52: LACM 64-16.2, left valve; Figure 51, interior (see Figure 3 for labeling of teeth); Figure 52, exterior.

bimodal anterior lateral teeth AII and AI that exhibit a tendency to form incipient cardinals 2a and 1.

Califadesma gen. nov. provides a more likely progenitor for the hinge of *Mesodesma* than does that of *Mactropsis*. The laterals of ***Califadesma*** are already bimodal, as are those of *Mesodesma* but not those of *Mactropsis*. ***Califadesma*** has a relatively larger resilifer that extends to the hinge plate margin and the tensilium was behind nymphs. The seat of the tensilium of *Mactropsis* is more internal than that of either ***Califadesma*** or *Mesodesma* and, although it might have migrated inward from a similar ancestral position, it would have had to remigrate to a more external position were *Mactropsis* ancestral to *Mesodesma*. Inward migration of tensilium and resilium is characteristic of mactrids (Saul, 1973), and the tensilifer position of *Mesodesma* can be derived from that of ***Califadesma*** by inward repositioning that includes loss of the nymph. The overall shape of *Mactropsis* is trigonal with the beaks located anterior to the midpoint (Figure 42) rather than donaciform with posteriorly placed beaks as are ***Califadesma*** and *Mesodesma*.

Dall (1898:907) noted that no shell characters unequivocally differentiate the Mesodesmatidae from the Mactridae, but ***Califadesma*** is sufficiently similar to *Meso-*

desma to be a mesodesmatid. *Mactropsis* falls not between ***Califadesma*** and *Mesodesma* in morphologic features, as its age might suggest, but is more similar in shape and hinge features to typical *Spisula* than to *Mesodesma*. The more trigonal mesodesmatids, such as *Paphies* Lesson, 1831, have smooth rather than the striated laterals of *Mactropsis*. As there are a number of relatively thick shelled mactrids including *Spisula solida* (Linnaeus, 1758), the thick shell of *Mactropsis* provides insufficient reason for placing this genus in the Mesodesmatidae.

Myadesma Clark, 1922, comprises four Pacific Slope species of Eocene to Miocene age: *M. eocenica* Clark, 1938; *M. howei* Clark, 1922 (Figures 85, 86); *M. dalli* Clark, 1922, type species by original designation (Figures 79–84); and *M. pacifica* (Hall & Ambrose, 1916), originally described as a *Mesodesma* (Figure 78). *Myadesma* has been included in Mesodesmatidae (Keen *in* Moore, 1969) or in Myadesmatidae (Clark, 1922; Beu, 1971). Myadesmatidae has been considered related to Mesodesmatidae of the Veneroida (Beu, 1971), Myidae of the Myoida (Clark, 1922; Hickman, 1969), or Periplomatidae of the Pholadomyoida (Clark, 1922). *Myadesma* resembles *Mesodesma* in its cuniform shape with the beaks near the posterior end, in having a well-marked, shallow pallial sinus (Figure 78), and in having anteriorly directed resilifers. The resilifers differ greatly from those of *Mesodesma* in that the resilifer of the left valve protrudes beyond the plane of the commissure (Figures 79, 81–84, 86) and that of the right valve is correspondingly sunken and lies against the valve (Figures 82, 83). The shape and position of the resilifers were seen by Clark (1922) as similar to those of Myidae. Additionally, within the resilifer of the left valve, Clark (1922) recognized a lithodesma that indicated to him a close relationship to Periplomatidae, and he suggested that Myidae should be included among anomalodesmaceans because of these similarities. Preservation of the type material is such that it is difficult to determine whether or not the lithodesma is in part fused to the dorsal side of the resilifer in the left valve; Clark (1922) said cemented. Beu (1971) indicated that it is fused to the resilifer of the left valve (Beu says "right valve," but he consistently uses right for left in his discussion of *Myadesma*). Matrix fills a narrow space between the resilifer and the lithodesma, but there is no well-demarked boundary between the posterodorsal half of the lithodesma and the ridge bounding the resilifer on its dorsal side. The hinge has been well described by Clark (1922); its structures do not resemble those of mactraceans. Not mentioned in any description is the consistent foramen in the beak of the right valve (Figures 82, 83). Similar wear holes are present in the pholadomyoid families Myochamidae, Periplomatidae, and Thraciidae. Such holes are not present in mactraceans or myaceans. I concur with Clark (1922) and Beu (1971) in placing this genus in the family Myadesmatidae Clark, 1922, and assign the family to the order Pholadomyoida Newell, 1965, and the superfamily Pandoracea Rafinesque, 1815.

Family Mesodesmatidae Gray, 1840

The shells of the Mesodesmatidae are said to differ from those of the Mactridae in being disproportionately heavy (Keen *in* Moore, 1969), but several genera with heavy shells are included in the Mactridae (*e.g., Spisula, Pseudocardium*), and some species of *Mesodesma* (*e.g., M. mactroides*) do not have a heavy shell. The siphons differ in the two families: those of Mesodesmatidae are naked and nearly or completely separated whereas in the Mactridae the siphons are united to their tips. As in the Mactridae, mesodesmatid hinges are arcticoid. Kalishevich (1967) incorrectly states that the resilifer of Mesodesmatidae is situated between the cardinal teeth, before cardinal 4b of the left valve. The resilifer of Mesodesmatidae is, however, placed as in Mactridae and is behind all cardinal teeth (see Figures 3, 45, 46, 50, 51) in both valves. In both Mactridae and Mesodesmatidae the cardinals are commonly crowded by the progressive enlargement and forward migration of the resilifer (Saul, 1973). The resilifer has rotated far forward in such mesodesmatid species as *Mesodesma donacium* and *M.* (*Ceronia*) *arctatum,* and the insignificant, fragile cardinal teeth are both readily overlooked and easily broken off, but in both valves all cardinals are on the anterior side of the resilifer. Typical mesodesmatids with striated laterals are compressed, cuneiform, and only moderately heavy. In the group with smooth laterals, which includes *Paphies,* the shell is more or less compressed, more commonly trigonal than cuneiform, and usually heavy.

The *Treatise on Invertebrate Paleontology* does not list Mesodesmatidae as being present in the Cretaceous, although *Ceroniola* Wilckens, 1904, is included by Keen (*in* Moore, 1969:N609) in this family. *Ceroniola* does not have mactroid hinge teeth. If it has a resilifer and is not related to ***Adelodonax,*** it may belong in the Quenstedtiidae.

Typical *Mesodesma* Deshayes, 1832, ranges from Pliocene to Recent (Herm, 1969); its subgenus *Ceronia* Gray, 1853, is known from Miocene to Recent (Beu & Rooij-Schuiling, 1982). *Donacilla* (*Mesodesma*) *sakhalinensis* Kalishevich, 1967, of late Eocene age differs from *Mesodesma* in lacking striations on its laterals and a posterior lateral in the left valve. If Kalishevich (1967:fig 2c) is correct and cardinal 4b is on the posterior side of the resilifer, *D.* (*M.*) *sakhalinensis* is not a mesodesmatid. Its affinities cannot be determined from the published figures.

Genus ***Califadesma*** Saul, gen. nov.

Type species ***Califadesma elafium*** Saul, sp. nov.

Diagnosis: A mesodesmatid with the resilifer posteriorly slanted and the two cardinal teeth on the hinge plate. Posteriorly the shell has a double siphonal fold.

Description: *Donax*-shaped bivalves of small size with sturdy shells, externally smooth except for fine growth lines. Valves elongate and compressed anteriorly, truncated

and inflated posteriorly having a double siphonal fold. Beaks low, very near posterior end. Hinge with posteriorly directed resilifer and flange-like nymph for the ligament; two cardinal teeth in each valve. Right valve with two thin lamellar cardinals 3a, 3b on either side of large socket, anterior to the resilifer; well-developed, elongate, dorsally striate anterior lateral AI and weaker, ventrally striate AIII very near shell margin; two short posterior laterals. Left valve with deltoid anterior cardinal 2b and very thin posterior cardinal 4b; anterior lateral well developed, striate dorsally and ventrally, very elongate; posterior lateral short, striate dorsally and ventrally. Pallial sinus a wide but shallow embayment.

Remarks: ***Califadesma*** differs from *Mesodesma* in having the resilifer posteriorly slanted and the cardinals upon the hinge plate. In *Mesodesma* the resilifer has moved to a more medial position and crowded the cardinals up off of the hinge plate onto a thin shelf overhanging the dorsal end of the resilifer (Figures 45, 46, 50, 51). The hinge of ***Califadesma***, with cardinals 3a, 3b, deltoid 2b, and 4b on the hinge plate, is more clearly mactroid (see Figure 3 for hinge diagrams) than is that of *Mesodesma*. SAUL (1988) erroneously reported that the laterals of these genera are striate only on the dorsal side, but AII and PII are finely striate on the ventral as well as the dorsal side, and AIII and PIII are finely striate on the ventral side in both *Mesodesma* and ***Califadesma***.

The posterior of ***Califadesma*** is clearly marked by a double siphonal fold, the ridges of which are more angulate on the right valve and more rounded on the left valve. Possibly the double siphonal fold in these shells is a reflection of the separate siphons.

Three species are here assigned to the genus ***Califadesma***: ***C. aspris*** sp. nov., ***C. elaphium*** sp. nov., and ***C. tuscanum*** sp. nov. All are from Upper Cretaceous deposits of northern California. The geologically oldest of these species, ***C. aspris***, is least cuneate and most mactriform.

The generic name is compounded of *Calif* for California and the Greek *desma*, meaning "band, bundle," from *Mesodesma* to which it is apparently related and perhaps antecedant. A generic name ending in *desma* is of neuter gender.

Califadesma aspris Saul, sp. nov.

(Figures 53–61)

Diagnosis: Relatively high, inflated ***Califadesma*** having abrupt posterior angulations and the ventral margin of the left valve overhanging that of the right valve.

Description: Shell small, moderately thick, broadly wedge-shaped. Valves compressed anteriorly, truncated and inflated posteriorly; posterior with strong double angulation; more anterior angulations sharper and stronger, especially in right valve; left valve noticeably more inflated than right valve. Dorsal margin straight; anterior margin squarely rounded; ventral margin convex, especially medially; posterior margin obtusely rounded and notched by sulcus between posterior two angulations. Beaks low, opisthogyral, very near posterior end. Lunule long, narrow, and slightly depressed.

Hinge with short, but well-developed flange-like nymph for external ligament and posteriorly directed resilifer immediately beneath beaks. Right valve with 3a and 3b very thin and lamellar, 3a scarcely detached from hinge margin and contiguous with long, thin, ventrally striate AIII; AI elongate; PI and PIII dorsally striate, short. Left valve with triangular 2b and very thin lamellar 4a adjacent to resilifer; AII bimodal, very long, lamellar, and striated; PII short, striated. Pallial line rather distant from valve margin; pallial sinus a wide but shallow indentation extending from posterior muscle scar to point ventrally below the beaks. Muscle scars subequal; posterior muscle scar round; anterior muscle scar elongate.

Holotype: LACMIP 7844, a large left valve.

Paratypes: LACMIP 7845 right valve from UCLA loc. 4104; 7846, a small right valve from CIT loc. 1893; 7847 medium left valve from CIT loc. 1893.

Dimensions: Of holotype LACMIP 7844 length 26.3 mm, height 18.8 mm, inflation of single valve 8.6 mm, beak 5.5 mm from posterior; paratype LACMIP 7845 length 23.8 mm, height 14.8 mm, inflation of single valve 4.9 mm, beak 4.6 mm from posterior; paratype LACMIP 7846 length 14.4 mm, height 9 mm, inflation of single valve 4 mm, beak 2.3 mm from posterior.

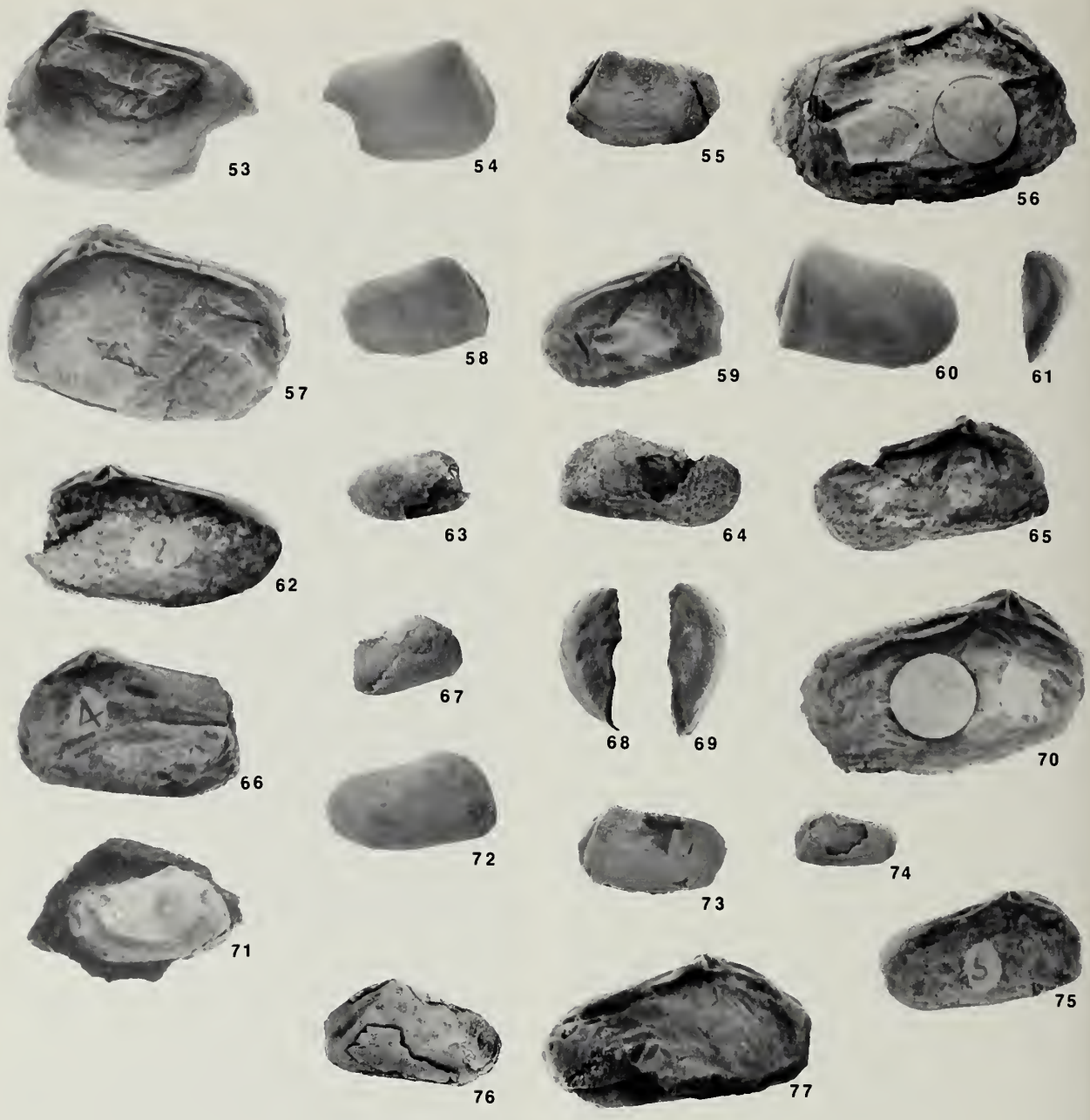
Type locality: LACMIP loc. 8133 (=UCLA loc. 4104, CIT loc. 1034, CIT loc. 1893), Oak Run, Millville Quadrangle, Shasta Co., California.

Distribution: Known only from the type locality.

Age: Coniacian, occurs with *Perissitys cretacea* (Cooper, 1896) and *Christitys delta* Popenoe & Saul, 1987.

Remarks: ***Califadesma aspris*** has the relatively highest, least elongate shell among donaciform bivalves discussed in this paper, and its ventral margin is the most convexly curved. The left valve is not only more inflated than the right valve, but the curved ventral margin of the left valve and its greater height to length ratio suggest that the ventral margin of the right valve fits within that of the left valve. Bilateral asymmetry may afford resistance to strong compressive forces during valve adduction and during attacks by shell-crushing predators (VERMEIJ, 1987:297). The loss of this characteristic between ***C. aspris*** and ***C. elaphium*** suggests that improved burrowing speed gained from a more streamlined, donaciform shape might have resulted in more escapes than did defensive armor, and thus have been of greater adaptive advantage.

Compared to ***Califadesma elaphium*** and ***C. tuscanum***, ***C. aspris*** has the most abrupt posterior angulations; these angulations diverge at the smallest angle, and the posterior margin is most noticeably sinused between the angulations.



Explanation of Figures 53 to 77

Figures 53–61. ***Califadesma aspris*** sp. nov. Figures 53, 54: LACMIP 7844 from LACMIP loc. 8133, holotype, left valve; Figure 53, interior, posterior valve margin broken, ×1.5; Figure 54, exterior, ×1. Figures 55, 56: LACMIP 7845 from UCLA loc. 4101, paratype, right valve; Figure 55, exterior, ×1; Figure 56, interior, ×2. Figures 57, 58: LACMIP 7847 from LACMIP loc. 8133, paratype, left valve; Figure 57, interior, tip of beak broken off, ×2; Figure 58, exterior, ×1. Figures 59–61: LACMIP 7846 from LACMIP loc. 8133, paratype, right valve, ×2; Figure 59, interior; Figure 60, exterior; Figure 61, posterior.

Figures 62–75. ***Califadesma elaphium*** sp. nov. Figures 62, 63: LACMIP 7849 from UCLA loc. 3622, paratype, left valve, posterior end broken off; Figure 62, interior, ×2; Figure 63, exterior, ×1. Figures 64, 65: LACMIP 7848 from UCLA loc. 3622, holotype, right valve; Figure 64, exterior, ×1.5; Figure 65, interior, ×2. Figures 66–68: LACMIP 7851 from UCLA loc. 3622, paratype, left valve, anterior end broken off; Figure 66, interior, ×2; Figure 67, exterior, ×1; Figure 68, posterior, ×2. Figures 69, 70, 73: LACMIP 7854 from UCLA loc. 4247, paratype, right valve; Figure 69, posterior, ×2; Figure 70, interior, ×2; Figure 73, exterior, ×1. Figure 71: LACMIP 7850 from UCLA loc. 3622, paratype, cast of left valve interior showing pallial line, pallial sinus, and adductor muscle scars, ×1.5. Figure 72: LACMIP 7857 from UCLA loc. 3633, paratype, left valve, exterior, ×2. Figures 74, 75: LACMIP 7852 from UCLA loc. 3622, paratype, right valve; Figure 74, exterior, ×1; Figure 75, interior, ×2.

Figures 76, 77. ***Califadesma tuscanum*** sp. nov., LACMIP 7858 from UCLA loc. 4082, holotype, right valve. Figure 76: exterior, ×1. Figure 77: interior, ×1.5.

The specific name is from the Greek *aspris*, a type of oak, and refers to the occurrence of this species on the north side of Oak Run.

Califadesma elafium Saul, sp. nov.

(Figures 15, 62–75)

Diagnosis: Moderately elongate ***Califadesma*** with rounded posterior angulations and the posterior margin barely sinused between the angulations.

Description: Shell small, thick, bluntly wedge-shaped. Beaks low, opisthogyral, very near posterior end. Dorsal margin straight, anterior margin bluntly rounded, ventral margin nearly straight subparallel to dorsal margin, posterior margin broadly rounded, sinused between posterior angulations. Valves compressed anteriorly, truncated and inflated posteriorly; posterior with double angulation, more anterior of angulations sharper and stronger. Lunule long, narrow, and slightly depressed.

Hinge with short but well-developed flange-like nymph for external ligament and posteriorly directed resilifer immediately beneath beaks. Right valve with 3a and 3b thin, lamellar; 3a scarcely detached from hinge margin; AI and AIII elongate; PI elongate; PIII short, low. Left valve with slightly bifid triangular 2b and very thin lamellar 4a adjacent to resilifer; AII very long and lamellar, bimodal; PII short, striated. Pallial line rather distant from valve margin; pallial sinus a wide but shallow indentation extending from posterior muscle scar to point ventrally below beaks. Muscle scars subequal; posterior muscle scar round; anterior muscle scar elongate.

Holotype: LACMIP 7848.

Paratypes: LACMIP 7849–7853 from UCLA loc. 3622, 7857 from UCLA loc. 3633, Chico Creek, Butte Co., California; LACMIP 7854–7856 from UCLA loc. 4247, Oak Run, Shasta Co., California

Dimensions: Of holotype, LACMIP 7848, length 18 mm, height 9.9 mm, inflation of single valve 3 mm, length beak to posterior 6 mm; of paratype LACMIP 7852, length 16 mm, height 8.5 mm, inflation of single valve 3.5 mm, length beak to posterior 5.5 mm; of paratype LACMIP 7854, length 21.7 mm, height 13 mm, inflation of single valve 5.4 mm, length beak to posterior 5.7 mm.

Type locality: UCLA loc. 3622, Chico Creek, Butte Co., California.

Distribution: Musty Buck Member of the Chico Formation on Chico Creek (UCLA locs. 3621–3623, 3625, 3627, 3628, 3633; LACMIP locs. 10849, 10850, abundant at 3622 and 3623), Butte Co.; Redding Formation (UCLA loc. 4247) south side of Oak Run, Shasta Co., California.

Age: Santonian.

Remarks: In external shape this species is very similar to *Notodonax* (*Aliodonax*) ***hsui*** and ***Adelodonax tectus*** with which it occurs on Chico Creek (Figures 14, 15). It differs from both in having the double posterior fold and sulcus, and from ***A. tectus*** in being more inflated and having the ventral and dorsal margins more nearly parallel. ***Califadesma elafium*** is more elongate and less inflated than ***C. aspris***, but less elongate and more inflated than ***C. tuscanum***. In ***C. elafium*** the posterior angulations are more rounded and diverge more widely than those of ***C. aspris***, and cardinal 3a is separated from lateral AII whereas in ***C. aspris*** these teeth are colaminal.

The specific name is from the Greek *elaphos* meaning "deer" or "stag," for its occurrence in the Musty Buck Member of the Chico Formation on Chico Creek.

Califadesma tuscanum Saul, sp. nov.

(Figures 76, 77)

Diagnosis: Elongate ***Califadesma*** of low inflation having the posterior margin straight between the angulations and with beaks at about the posterior third of the shell.

Description: Shell small, thick, bluntly wedge-shaped. Beaks low, opisthogyral, very near posterior end. Dorsal margins straight, sloping; anterior margin bluntly rounded; ventral margin nearly straight, subparallel to dorsal margin; posterior margin nearly straight between angulations, obtusely rounded. Valves compressed anteriorly, truncated and moderately inflated posteriorly; posterior with double, rounded angulations. Lunule long, narrow, and slightly depressed.

Hinge of right valve with short flange-like nymph for external ligament and posteriorly directed resilifer immediately beneath beaks. Cardinal teeth 3a and 3b thin, lamellar; 3a scarcely detached from hinge margin; AI and AIII elongate; PI elongate, PIII low, elongate.

Holotype: LACMIP 7858.

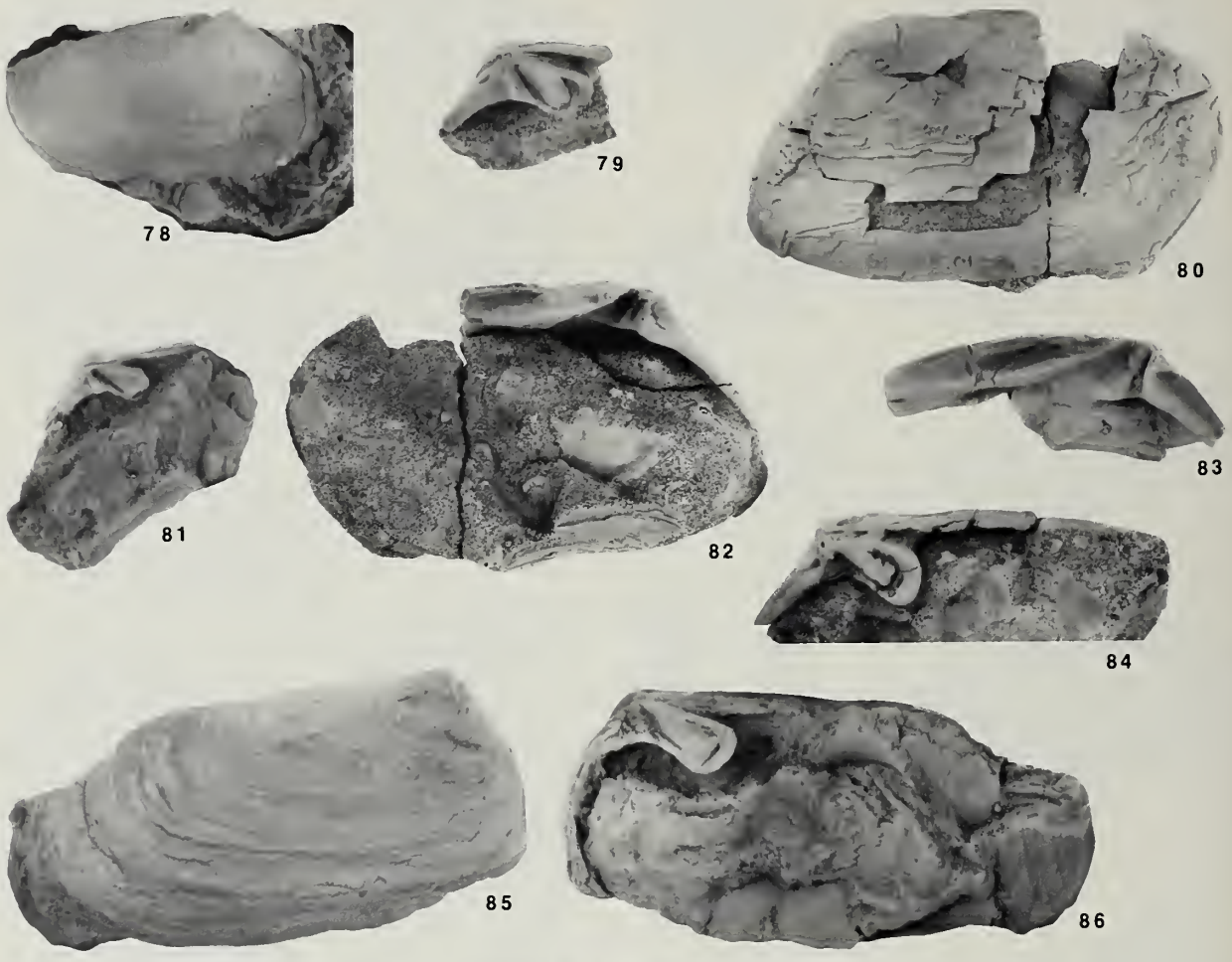
Dimensions: Of holotype, length 27 mm, height 14.6 mm, thickness 5.8 mm, length beak to posterior 9.2 mm.

Type locality: UCLA loc. 4082, Tuscan Springs, Tehama Co., California.

Distribution: Known only from the Chico Formation at Tuscan Springs, on Little Salt Creek, Tehama Co., California.

Age: Campanian.

Remarks: This species is described from a single right valve lacking most of its shell. The specimen preserves the valve shape, the placement of the double posterior angulation, and most of the hinge teeth which have been only partially exposed as more cleaning of the hinge would



Explanation of Figures 78 to 86

Figure 78. *Myadesma pacifica* (Hall & Ambrose, 1916), CAS 61804.01 from Alameda Creek, Alameda Co., California, holotype, left valve, pallial line and sinus, ×1, middle Miocene.

Figures 79–84. *Myadesma dalli* Clark, 1922, Vancouver Island, British Columbia, upper Oligocene (MOORE, 1984, includes the Sooke Formation in the Juanian Stage), ×1. Figure 79: CAS 61805.04, paratype, left valve hinge with lithodesma? in salient resilifer. Figures 80, 82: CAS 61805.01, holotype, right valve; Figure 82, showing foramen in beak and deeply depressed resilifer. Figure 81: CAS 61805.02, paratype, hinge of left valve. Figure 83: CAS 61805.03, paratype, hinge of right valve showing foramen in beak. Figure 84: CAS 231.01, paratype, hinge of left valve with lithodesma? in salient resilifer.

Figures 85, 86. *Myadesma howei* Clark, 1922, UCBMP 30328 from UCB loc. 3622, near Eugene, Oregon (HICKMAN, 1969:73, did not collect this species from the Eugene Formation and considers its occurrence there questionable), lower Oligocene, holotype, left valve, ×1. Figure 85: exterior. Figure 86: hinge.

break the specimen. The pallial line and posterior adductor muscle scar are not apparent on this specimen, but the position of the anterior adductor muscle scar can be determined. The outline of GABB's (1864:pl. 23, fig. 138) *Tellina quadrata,* a species GABB (1864:159) described from a single Tuscan Springs specimen that he considered to be a right valve, resembles that of ***Califadesma tuscanum***. Gabb wrote "muscle scars and pallial sinus almost invisible on cast" and did not draw muscle scars or pallial line on his figure. He considered that the beak was nearer the obliquely subtruncated anterior end and did not mention the presence of a double fold on the posterior slope. STEWART (1930:7) was unable to find Gabb's original material, and Gabb's statements suggest that despite the similar outline and same type locality ***C. tuscanum*** is not *T. quadrata.*

Califadesma tuscanum differs from ***C. elaphium*** in having beaks farther from the posterior end and being less inflated. It differs from ***C. aspris*** in having a nearly straight ventral margin. Of the three species, it has the lowest, most divergent posterior angulations.

Molluscan species extracted from the pebbly sandstone at Tuscan Springs are indicative of diverse shallow-into-deep-water habitats. RUSSELL *et al.* (1986:190) consider these deposits to be a debris flow containing a shallow marine fauna comparable to their *Cymbophora suciensis*

assemblage. Collections include, however, species and genera typical of both deeper and shallower water than that assemblage; and no collection I have used contains *Cymbophora suciensis*. The presence of the littoral ***Califadesma tuscanum*** in these probable outer shelf deposits strongly suggests down slope displacement.

The species is named for its type locality, Tuscan Springs, Tehama Co., California, a spa on Little Salt Creek at the turn of the century (WARING, 1915:289).

ACKNOWLEDGMENTS

W. P. Popenoe and L. R. Saul were planning to jointly describe those species that occurred both in the Redding area, Shasta Co., and at Chico Creek, Butte Co., California, and we both worked on hinges of *Califadesma elaphium*, *Notodonax* (*Aliodonax*) *hsui*, and *Adelodonax tectus*, but Popenoe left no descriptions of these species. I gratefully acknowledge his efforts in cleaning some of the hinges, and his helpful and entertaining discussions regarding these species. Eduardo Olivero kindly and graciously provided photocopies of pertinent pages from FERUGLIO (1936). Alan Beu brought to my attention STINNESBECK's (1986) recent paper on the Quiriquina fauna and considerately sent photocopies of important pages. Specimens from the Cabrillo Formation on Mt. Soledad, San Diego Co., California, were collected and donated by M. P. Kennedy; specimens from the Rosario Formation on Punta Banda, Baja California, Mexico, were collected and donated by J. M. Alderson. Figures 1 and 2 were drafted by Edward Barros, Jr.; the hinges of Figure 3 were drawn by W. S. Griswold. Helpful criticism of this paper has been provided by Eugene Coan, J. R. Harris, G. L. Kennedy, E. C. Wilson, and an anonymous reviewer.

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APPENDIX 1

LOCALITIES CITED

Geographic areas of the cited localities are plotted on Figure 1. Type localities of species described in this paper are fully described. Previously published localities are briefly characterized and the reference given.

213 CAS: 12 mi. W of Sooke, in the seacliff immediately E of the mouth of Coal [Kirby] Creek, Vancouver Island, British Columbia. Sooke Formation. Oligocene.

3314 UCLA: Float in creek bed at UCLA loc. 3313, S side Deer Valley, 2100′S, 28°W of NE cor. sec. 24, T1N, R1E, Antioch South Quad., Contra Costa Co., Calif. 37°55′11″N, 121°48′26.5″W. Coll.: W. P. Popenoe, August 1944. Great Valley Series, Deer Valley Formation of Colburn. Late Maastrichtian.

3621 UCLA: E of Chico Creek Co. road in upper part of meadow to N of old prune orchard, 2050′S, 2350′W of NE cor. sec. 12, T23N, R2E, Paradise Quad., Butte Co., Calif. 38°52′07″N, 121°42′05″W. Coll.: L. R. & R. B. Saul, 1952. Chico Formation, Musty Buck Member. Early Santonian.

3622 UCB: Smith's Quarry, between Millrace and Franklin Blvd., Eugene, 0.7 mi. E of BM 449, sec. 33, T17S, R3W, Oregon. Eugene Formation. Oligocene.

3622 UCLA: First ravine to S of Mickey's Place on "trail" about 0.2 mi. above W side Chico Creek, approx. 800′N, 1400′E of SW cor. sec. 1, T23N, R2E, Paradise Quad., Butte Co., Calif. 39°52′27″N, 121° 42′24″W. Coll.: L. R. & R. B. Saul, 1952. Chico Formation, Musty Buck Member. Early Santonian.

3623 UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. 39°51′51″N, 121°42′29″W. Chico Formation, Musty Buck Member. Early Santonian. (MATSUMOTO, 1960:155)

3624 UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. 39°52′28″N, 121°42′31″W. Chico Formation, Musty Buck Member. Early Santonian. (POPENOE & SAUL, 1987:35)

3625 UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. 39°51′47″N, 121°42′33″W. Coll.: L. R. & R. B. Saul, 1952. Chico Formation, Musty Buck Member. Early Santonian. (POPENOE *et al.*, 1987:99)

3627 UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. 39°51′26″N, 121°42′32″W. Chico Formation, Musty Buck Member. Late Santonian. (MATSUMOTO, 1960: 156)

3628 UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. 39°51′19″N, 121°42′33″W. Coll.: L. R. & R. B. Saul, 1952. Chico Formation, Musty Buck Member. Santonian. (POPENOE *et al.*, 1987:99)

3633 UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. 39°51′14″N, 121°42′24″W. Chico Formation, top of Musty Buck Member. ?Late Santonian, *Baculites capensis* Zone. (MATSUMOTO, 1960:15, 156)

3958 UCLA: S side of Deer Valley, sandstone lens in conglomerate, same ridge as UCLA 3957, but about 700′ farther S along crest of ridge, 2350′N, 750′W of SE cor. sec. 24, T1N, R1E, Antioch South Quad., Contra Costa Co., Calif. 37°55′01.5″N, 121°48′24″W. Coll.: W. P. Popenoe, 1944. Great Valley Series, Deer Valley Formation of Colburn, 1964. ?Late Maastrichtian.

3959 UCLA: Hard sandstone outcrop on crest of same ridge as UCLA loc. 3957, 400′S of UCLA loc. 3957, S side Deer Valley, 2580′S, 690′W of NE cor. sec. 24, T1N, R1E, Antioch South (1953) Quad., Contra Costa Co., Calif. 37°55′04″N, 121°48′23.5″W. Coll.: W. P. Popenoe, 1944. Great Valley Series, Deer Valley Formation of Colburn, 1964. ?Late Maastrichtian.

3960 UCLA: Hard sandstone bed just above conglomerate, S side of Deer Valley on first ridge W of UCLA locs. 3957, 3958, 3959, 2550′S, 35°W of NE cor. sec. 24, T1N, R1E, Antioch South Quad., Contra Costa Co., Calif. Probably same bed as UCLA 3958. 37°55′08″N, 121°48′34″W. Coll.: W. P. Popenoe, 1944. Great Valley Series, Deer Valley Formation of Colburn, 1964. ?Late Maastrichtian.

4082 UCLA: Tuscan Springs, on Little Salt Creek, about 10 mi. NE of Red Bluff, approx. 900′S, 1650′W of NE cor. sec. 32, Tuscan Springs Quad., Tehama Co., Calif. 40°14′29″N, 122°06′35″W. Chico Formation.

Early Campanian. (STEWART, 1927:292; SAUL, 1978: 57)

4104 UCLA: N side of Oak Run, Millville Quad., Shasta Co., Calif. 40°37′53″N, 122°06′W. Redding Formation, Member IV of Popenoe. Coniacian. (POPENOE & SAUL, 1987:36)

4106 UCLA: N of Clover Creek, Millville Quad., Shasta Co., Calif. 40°37′20″N, 122°03′26″W. Redding Formation. Early Santonian. (POPENOE, 1983:760, 765)

4247 UCLA: SE side of Oak Run, about 600′N, 1600′E of SW cor. sec. 15, T32N, R2W, Millville Quad., Shasta Co., Calif. 40°37′30″N, 122°04′52″W. Coll.: W. P. Popenoe, 31 Aug. 1959. Redding Formation, Member V in coarse gritty sandstone about 50′ below base of thick conglomerate bed. Early Santonian.

4347 UCLA: Sandstone cropping out below high tide line about 0.5 mi. N of Bolsa Point and just S of Spring Bridge Gulch, Pigeon Point Quad., San Mateo Co., Calif. 37°12′16″N, 122°24′16″W. Coll.: L. R. & R. B. Saul, 1947. Pigeon Point Formation. Campanian.

4671 UCLA: Sandstone cropping out along ridge top 100–200′ below base of Paleocene, S side Deer Valley, 2200′S, 600′W of NE cor. sec. 24, T1N, R1E, Antioch South (1953) Quad., Contra Costa Co., Calif. 37°55′06.5″N, 121°48′23.5″W. Coll.: W. P. Popenoe, 1962. Great Valley Series, Deer Valley Formation of Colburn, 1964. Late Maastrichtian.

5659 LACMIP: Little Stave Creek, shells and shark's teeth in light gray-green glauconitic sand and silt, approx. 5′ above base of 25′ cliff at end of 0.25-mi. long trail which begins at W end of West Point Drive near University of Alabama Historical Marker, Clark Co., Alabama. Coll.: Bruce & Joann Welton, 4 Sept. 1975. Claiborne Group, Gosport Sand. Middle Eocene.

6359 UCLA: W side San Joaquin Valley, just S of Salado Creek, 2000′S, 2650′E of NW cor. sec. 15, T6S, R7E, Orestimba Quad., Stanislaus Co., Calif. 37°24′57″N, 121°11′12″W. Coll.: R. B. Stewart & W. P. Popenoe, 1944. Moreno Formation, Garzas Sand. Maastrichtian.

6360 UCLA: W side San Joaquin Valley, draw S of Black Gulch, 1700′S, 1850′E of NW cor. sec. 34, T5S, R7E, Orestimba Quad., Stanislaus Co., Calif. 37°27′34″N, 121°11′21″W. Coll.: R. B. Stewart & W. P. Popenoe, 1944. Moreno Formation, Garzas Sand. Maastrichtian.

6489 UCLA: 3750′S, 14°E of buildings on Moffett Ranch in Orestimba Creek, in medium grained pepper-and-salt sandstone on crest of long N–S ridge near N end, 2490′S, 1000′E of NW cor. sec. 35, T7S, R7E, Orestimba Quad., Stanislaus Co., Calif. 37°17′N, 121°10′32″W. Coll.: W. P. Popenoe, 29 Aug. 1944. Moreno Formation, Garzas Sand. Maastrichtian.

7137 UCLA: Fossiliferous, hard calcareous concretion from sandstone beds in graben? (*Coralliochama* beds in sea cliff on both sides of graben?) about 200′ eastward along shore from sandy ravine with road to beach, N side Punta Banda Peninsula, Baja California Norte, Mexico. Coll.: John Alderson, 18 March 1984. Rosario Formation. Early Maastrichtian.

8133 LACMIP (=CIT loc. 1034, UCLA loc. 4104): Hard, cemented sandstone slabs weathering out of siltstone in pasture a little W of N of Hathaway Ranch house, about 1500′S, 1400′E of NW cor. sec. 16, T32N, R2W, Millville Quad., Shasta Co., Calif. 40°37′53″N, 122°06′W. Coll.: W. P. Popenoe & W. Findlay, 1933. Redding Formation, Member IV of Popenoe. Coniacian.

8148 LACMIP (=CIT loc. 1896): Type Garzas, Garzas Creek, Pacheco Pass Quad. (1947), Stanislaus Co., Calif. Approx. 37°13–15′N, 121°07–09′W. Coll.: W. P. Popenoe, 1944. Moreno Formation, Garzas Sand. Maastrichtian.

10846 LACMIP (=CIT loc. 1014): Right bank of Chico Creek, about 1 mi. upstream from bridge across creek below Mickey's house, NE ¼ sec. 1, T23N, R2E, Paradise Quad., Butte Co., California. Coll.: Popenoe and Scharf, 6 Aug. 1931. Chico Formation, Ponderosa Way Member. ?Coniacian.

10847 LACMIP (=CIT loc. 1016): Chico Creek, Paradise Quad., Butte Co., Calif. 39°52′28″N, 121°42′28″W. Coll.: L. R. & R. B. Saul, 1952. Chico Formation, Musty Buck Member. Early Santonian.

10849 LACMIP (=CIT loc. 1017): W side of Chico Creek, Paradise Quad., Butte Co., Calif. 39°52′47″N, 121°42′23″W. Chico Formation, Musty Buck Member. Santonian (POPENOE *et al.*, 1987:98)

10850 LACMIP (=CIT loc. 1313): E side Chico Creek, Paradise Quad., Butte Co., Calif. Approx. 39°51′38″N, 121°42′18″W. Chico Formation, Musty Buck Member. Santonian (POPENOE *et al.*, 1987:99)

28629 LACMIP: S of Easter Cross on W side of ridge which extends S from Mt. Soledad along W side of Rose Canyon, S of prominent amphitheater facing Rose Canyon, 7050′N of T16S, 1100′E of R3W, La Jolla Quad., San Diego Co., Calif. 32°50′15.1″N, 117°13′59″W. Coll.: M. P. Kennedy, 1967? Cabrillo Formation. Maastrichtian.

61804 CAS: Alameda Creek, 1.5 mi. S of Welch Cr., Pleasanton Quad., Alameda Co., Calif. Monterey Sandstone. Mid Miocene.

61805 CAS: Seacliffs between mouths of Muir and Coal Creeks, W of Otter Point, Sooke, Vancouver Island, British Columbia. Sooke Formation. Oligocene.

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Revision on Shallow-Water Species of the Genus *Placiphorella* (Polyplacophora: Mopaliidae) from Japan

by

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Abstract. Three species of the chiton genus *Placiphorella* are recognized in the intertidal and sublittoral zones of Japan: *P. borealis* Pilsbry, 1893, recorded for the first time from Japan proper; *P. stimpsoni* (Gould, 1859) (=*P. japonica* (Dall, 1925)); and *P.* ***borealijaponica*** sp. nov., examples of which have been confused previously with *P. stimpsoni*. The shells, radula, girdle elements, and digestive tract of each species are described and illustrated.

INTRODUCTION

The so-called veiled chitons, of the Polyplacophoran genus *Placiphorella* (Carpenter MS) Dall, 1879, are peculiar in having depressed and wide valves, anteriorly expanded girdle with scaled bristles, and fingerlike projections of the pallial fold. One of the species, *P. velata* (Carpenter MS) Dall, 1879, was observed to be carnivorous with a peculiar trapping behavior (McLean, 1962). However, the biology of most of the species has never been worked out.

Nine species have hitherto been known from the Pacific Ocean and one from the Atlantic Ocean. In the Pacific Ocean, except for *Placiphorella blainvillii* (Broderip, 1832), eight species among nine are distributed in the North Pacific. From Japan and its adjacent waters, five species have been described, and three species among them—*P. stimpsoni* (Gould, 1859), *P. borealis* Pilsbry, 1893, and *P. japonica* (Dall, 1925)—are regarded as shallow-water dwellers, while the other two—*P. uschakovi* Yakovelva, 1952, and *P. albitestae* Is. Taki, 1954—are deep-water members that are not treated in this paper.

Since their original description, several subsequent authors, including Plate (1901), Berry (1917), Taki (1938, 1954), Leloup (1942), Yakovleva (1952), and Wu & Okutani (1985), have redescribed them. However, no work based on direct comparison of large numbers of specimens has been done.

The present paper describes the morphological characters of each species and clarifies nomenclatural confusion by a critical examination of type materials of these three species and over 100 specimens collected from various localities in Japan.

MATERIALS AND METHODS

The numbers of specimens examined by species, locality, size, and source are given in Tables 1–4.

Most of the specimens collected by us were fixed in 10% formalin when collected and preserved in 40% isopropyl alcohol.

Observations were made with a stereoscopic dissection microscope and photomicroscope. A scanning electron microscope was used to observe the microstructure of girdle elements and radulae.

Slide calipers were used to measure animal bodies and valves. Girdle elements and radulae were measured with the aid of an eyepiece micrometer.

Drawings were executed with the aid of an eyepiece micrometer and/or camera lucida.

Observed spicules of the perinotum, margin, and hyponotum of most specimens were removed from the middle portion of the body. In observing radulae, the tenth to twentieth transverse rows from the anterior were selected.

The terminology in this paper mostly follows Taki (1938), especially for radular features, and Kaas & Van Belle (1985). However, a few specified terminology used in this paper are as follows:

Pectinate or *pectination:* The basic morphology implied by the word pectination (or being pectinate) is not essentially different from how it is used for other chitons. However, pectinations in *Placiphorella* are quite different from those in the family Chitonidae, in which they are finer, deeper, and more numerous than those of *Placiphorella.*

Prop plate: A small process of the central tooth, extending anteriorly and supporting this tooth. Terms referring to

Table 1

Data of specimens of *Placiphorella borealis* used in this study.

Locality	Number of individuals	VL (mm)	Date collected	Source
Bering Sea				
Bering Island	1	—	—	USNM 106922 (holotype)
Pacific Coast (all SE Hokkaido)				
Nosappu	7	16.6–34.8	12 June 1987	S. Murakamki
Kiritappu	2	24.7, 27.1	11 June 1987	S. Murakamki
Akkeshi	1	20.9	7–8 July 1987	Y. Kuwahara
Akkeshi	2	12.5, 14.9	10 July 1982	Y. Kuwahara
Akkeshi	4	9.4–16.8	9 July 1983	Y. Kuwahara
Akkeshi	2	18.1, 19.6	13 July 1983	Y. Kuwahara
Erimo	6	14.4–23.0	14 June 1987	S. Murakami

VL, valve length.

the direction of the radular parts are used to indicate the state of withdrawal of the radular ribbon. Thus, for example, the cusp of the major lateral is directed "posteriorly."

Valve length: The distance from the anterior tip of the head valve to the posterior tip of the tail valve.

The abbreviations used in this paper for institutions and museums are as follows:

CASIZ—California Academy of Sciences, Department of Invertebrate Zoology, San Francisco.
NSMT—National Science Museum, Tokyo.
USNM—United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Family Mopaliidae Dall, 1889

Genus *Placiphorella* (Carpenter MS) Dall, 1879

Type species: *Placiphorella velata* (Carpenter MS) Dall, 1879 by O.D.

Placiphorella borealis Pilsbry, 1893

(Figures 1–10, 47, 48)

Placiphorella stimpsoni: Dall, 1886:210 (in part, *non* Gould, 1859).
Placiphorella borealis Pilsbry, 1893:309–310, pl. 66, figs. 14–17; Yakovleva, 1952:75–76, fig. 35, pl. 5, fig. 3.

Materials examined: See Table 1.

Table 2

Data of specimens of *Placiphorella* ***borealijaponica*** Saito & Okutani, sp. nov. used in this study.

Locality (all Hokkaido)	Number of individuals	VL (mm)	Date collected	Source
Pacific Coast				
Akkeshi	2	25.5, 27.5	10 July 1983	Y. Kuwahara
Muroran	2	23.4, 24.8	5 Sept. 1976	Y. Kuwahara
Muroran	2	24.5, 26.3	10 Aug. 1983	Y. Kuwahara
Muroran	1	24.1	16 Aug. 1987	H. Saito
Hakodate	2	9.0, 22.5	14 June 1978	Y. Kuwahara
Okhotsk Sea				
Kitami-Esashi	4	11.2–15.2	11 Aug. 1987	H. Saito
Japan Sea				
Rebun Island	1	17.5	13 Aug. 1987	H. Saito
Hashibetsu	1	21.0	14 Aug. 1987	H. Saito
Kemafure	1	25.0	17 Aug. 1986	H. Saito
Hamamasu	4	10.0–34.0	17 Aug. 1986	H. Saito
Otamoi	3	19.0–29.5	16 Aug. 1986	H. Saito
Oshoro	2	26.0, 26.0	30 Sept. 1982	Y. Kuwahara
Oshoro	17	9.0–31.8	18 Aug. 1987	H. Saito

VL, valve length.

Table 3

Data of type series of *Placiphorella* ***borealijaponica*** sp. nov.

	BL (mm)	BW (mm)	VL (mm)	WIV (mm)	Locality	Date collected
Holotype	38.0 (curled)	33.4	33.4	20.8	Hamamasu	17 Aug. 1986
Paratype 1	45.6	34.4	34.0	23.3	Hamamasu	17 Aug. 1986
Paratype 2	37.8	29.5	30.0	22.0	Oshoro	18 Aug. 1987
Paratype 3	37.7	25.9	24.1	18.5	Muroran	16 Aug. 1987
Paratype 4	24.2	16.6	17.5	10.3	Rebun Id.	13 Aug. 1987
Paratype 5	29.3	23.0	21.8	16.0	Oshoro	18 Aug. 1987
Paratype 6	27.9	20.2	21.0	15.5	Hashibetsu	14 Aug. 1987
Paratype 7	30.0	24.5	21.8	18.0	Oshoro	18 Aug. 1987
Paratype 8	22.5 (curled)	22.3	20.5	16.8	Oshoro	18 Aug. 1987

BL, body length; BW, body width; VL, valve length; WIV, width of valve IV.

Description: Body oval in outline, valves depressed, subcarinate, side slopes nearly straight; girdle widely extended anteriorly, uniformly brown to dark yellowish brown in color (Figures 1, 47).

Valves: Head valve (Figure 3) thick, crescent-shaped, anterior slope straight to slightly concave, with small roundish notch and slightly raised apex, posterior margin of both sides slightly convex; tegmental surface sculptured with numerous, very low, radiating riblets and concentric growth lines; interior smooth, thickened anteriorly; insertion plates short, thickened at both sides of each slit, and somewhat pectinate; usually 8 slits but up to 11; slit rays appear as white lines.

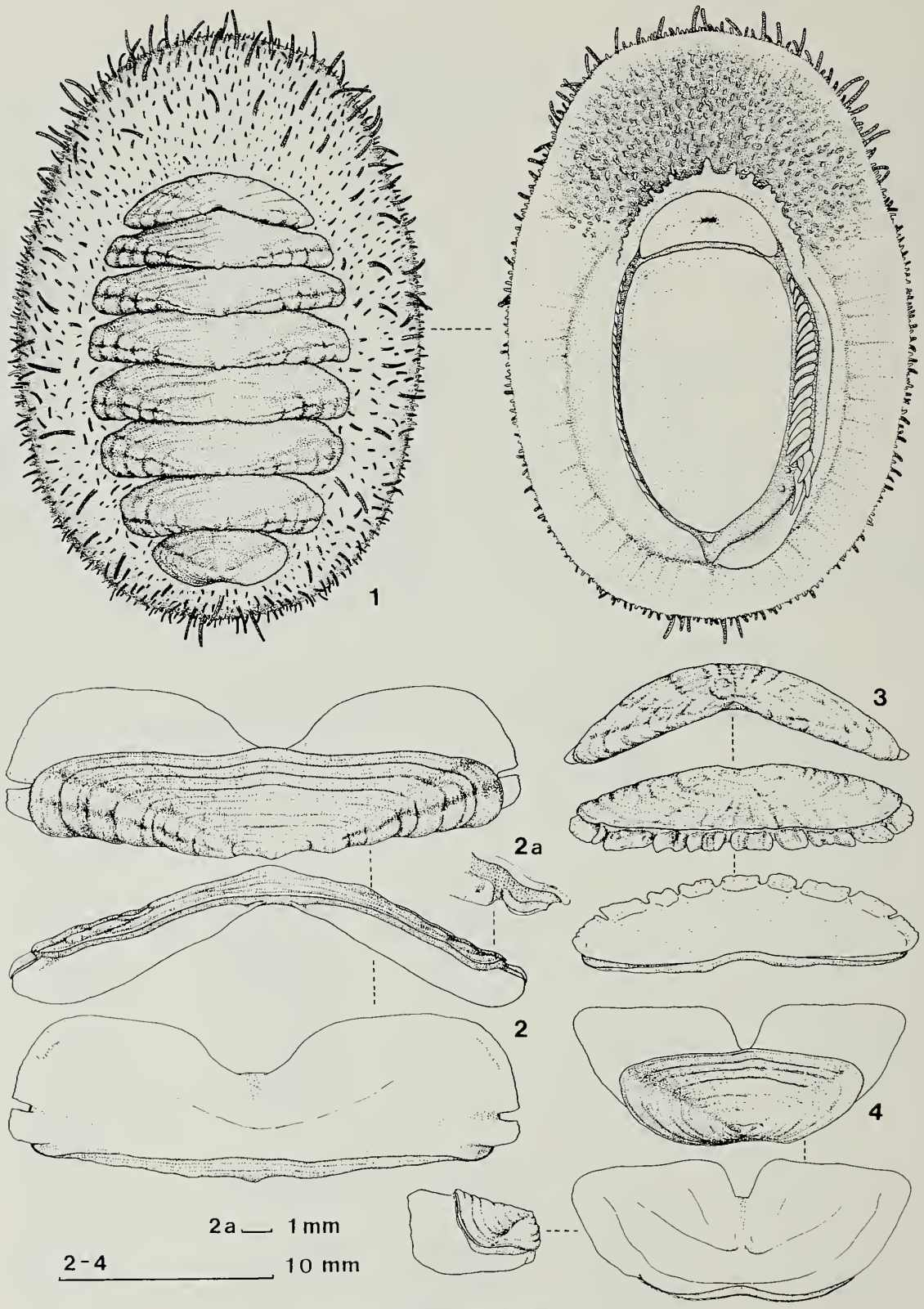
Intermediate valves (Figure 2) oblong in outline, much

Table 4

Data of specimens of *Placiphorella stimpsoni* used in this study.

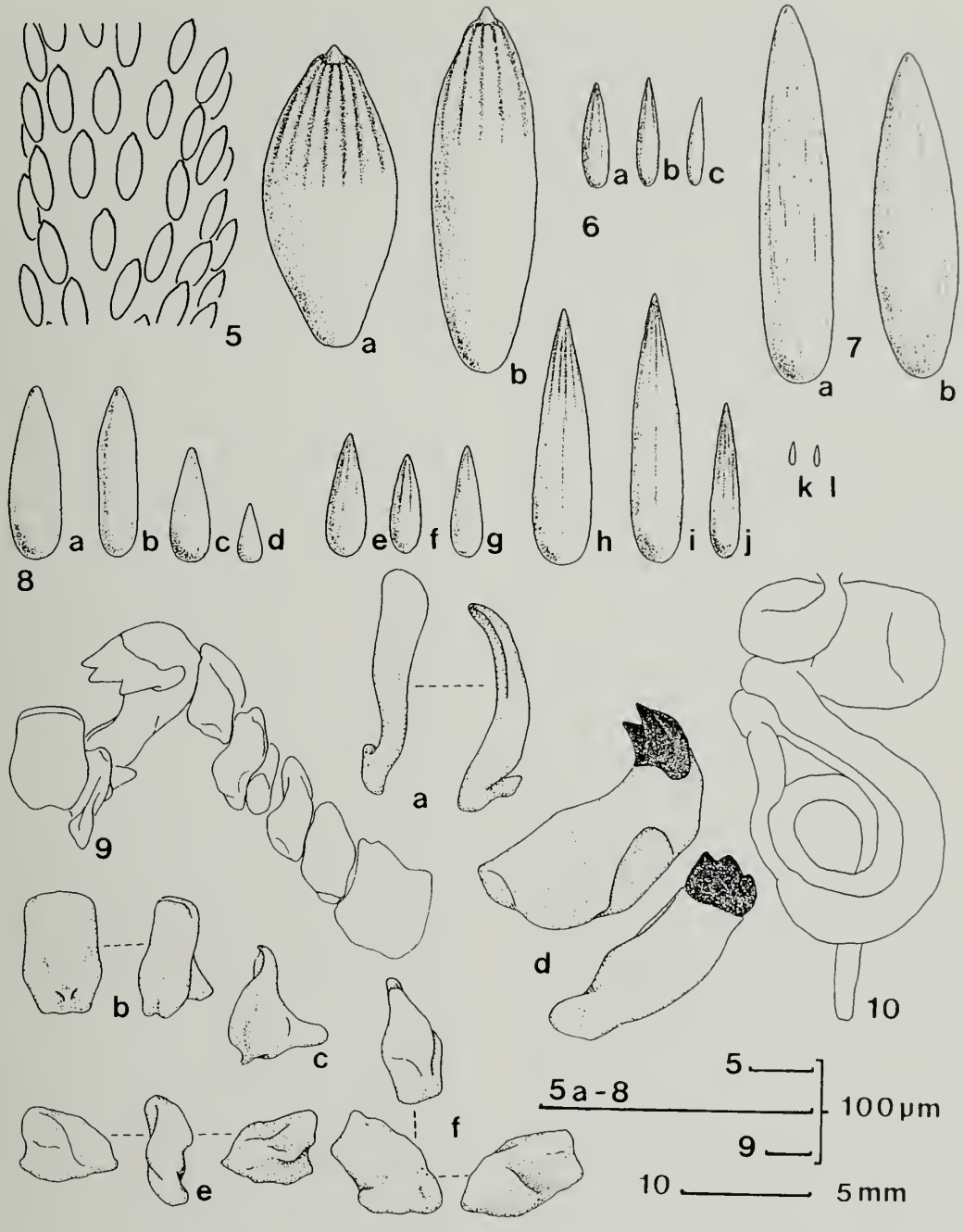
Locality	Number of individuals	VL (mm)	Date collected	Source
Pacific Coast				
"Hakodadi" Bay (Hakodate)	2	18.6, 24.5	—	USNM 1646 (syntypes)
"Emi Bashiu" (Emi, Boso Pen.)	2	20.3, 35.0	—	USNM 333541 (syntypes)*
Ozuchi, NE Honshu	2	15.3, 22.3	12–19 June 1983	Y. Kuwahara
Ozuchi, NE Honshu	1	18.2	—	T. Okutani
Okirai, NE Honshu	8	12.5–26.2	25 June 1987	S. Murakami
Banda, Boso Pen.	1	15.8	24 Apr. 1986	H. Saito
Banda, Boso Pen.	2	9.3, 24.8	5 June 1986	H. Saito
Banda, Boso Pen.	1	17.8	5 Mar. 1987	H. Saito
Manazuru, Sagami Bay	2	26.3–31.8	29 Nov. 1987	H. Saito
Shimoda, Izu Pen.	1	33.2	7 Aug. 1987	H. Saito
Shimoda, Izu Pen.	1	44.5	11 Sept. 1987	H. Saito
Shimoda, Izu Pen.	4	13.9–33.4	16–18 May 1988	H. Saito
Sumoto, Inland Sea	1	31.5	8 Dec. 1985	H. Saito
Iyo, Inland Sea	2	—	—	USNM (no cat. number)
Yokonami Pen., Shikoku	7	17.0–28.0	3 Nov. 1985	H. Saito
Yokonami Pen., Shikoku	2	12.6, 17.7	1 Jan. 1986	H. Saito
Japan Sea				
Asamushi, Mutsu Bay	6	19.5–31.6	6 Sept. 1986	S. Murakami
Fukuura, N Honshu	4	17.3–21.3	21 June 1987	S. Murakami
Fukuoka, Kyushu	1	25.6	27 Apr. 1987	S. Nishihama
East China Sea				
Amakusa, Kyushu	1	22.5	8 Aug. 1987	S. Nishihama

VL, valve length; *, *Langfordiella japonica* Dall, 1925.



Explanation of Figures 1 to 4

Figures 1–4. *Placiphorella borealis* Pilsbry, 1893. Valve length 33.8 mm, from Nosappu. Figure 1: dorsal and ventral views of animal. Figure 2: valve IV, dorsal, anterior and ventral views. Figure 2a: valve IV, lateral portion. Figure 3: head valve, dorsal, anterior and ventral views. Figure 4: tail valve, dorsal, ventral and lateral views.



Explanation of Figures 5 to 10

Figures 5–10. *Placiphorella borealis* Pilsbry, 1893. Figures 5–9: valve length 33.8 mm, from Nosappu; Figure 10, valve length 23.0 mm, from Erimo. Figure 5: bristle, arrangement of spicules. Figures 5a, b: spicules of bristle. Figures 6a–c: spicules on perinotum. Figures 7a–c: marginal spicules. Figures 8a–d: spicules on hyponotum. Figures 8e–g: spicules on pallial fold. Figures 8h–j: spicules on fingerlike projection. Figures 8k, l: spicules on papilla. Figure 9: half radula row (major uncinus is removed except for basal plate). Figure 9a: major uncinus, posterior and lateral views. Figure 9b: central, anterior and lateral views. Figure 9c: centro-lateral, lateral view. Figure 9d: major lateral, outer lateral and dorsal views. Figure 9e: outer small lateral, inner lateral, dorsal and outer lateral views. Figure 9f: inner small lateral, dorsal, inner and outer lateral views. Figure 10: digestive tract, dorsal view.

wider than long, valve IV widest, subcarinate, not beaked posteriorly, slightly bending anteriorly in middle of jugal sinus; lateral areas with strong diagonal and sutural ribs, both clearly separated from each other by distinct groove; central area nearly smooth except for concentric growth lines; interior smooth with transverse callus extending from center to near slits and slightly convex anteriorly; slit rays with shallow, fine grooves; sutural laminae very wide, rather thin, gently convex and sharp at anterior edge, separated by wide jugal sinus and usually scarcely connected across jugum; insertion plates thick, short but the longest among species of this genus so far known and extending beyond narrow eaves, hardly pectinate laterally; insertion plates and sutural laminae (Figure 2a) thickened and curved dorsally on sides of slit.

Tail valve (Figure 4) comparatively large for genus, depressed, roughly oval in outline, its greatest width including articulamentum nearly equal to tegmental width of head valve; anterior margin of tegmentum regularly convex and elevated without false beak; mucro distinct, slightly raised, situated near posterior third with convex or straight frontal slope; central area without sculpture except for concentric growth lines; posterior area clearly defined, gradually descending posteriorly; posterior margin shallowly sinuate; interior callused posteriorly; sutural laminae broad, truncated anteriorly, separated by jugal sinus; insertion plates very short, posterior margin slightly pectinate; one slit per side.

Girdle: Perinotum densely covered by minute and slender spicules (Figures 6a–c) with weakly striated distal portion ending in pointed tip, brownish yellow in color, 25–45 μm in length; bristles on side of sutures (Figure 5) somewhat larger than others; each bristle with smooth surface, composed of small, depressed, ellipsoidal spicules (Figures 5a, b) papillated at tip, deeply striated, brownish, 90–120 μm in length, arranged in oblique series around axis and not imbricating each other; slightly smaller bristles closely set near anterior margin and posterior to tail valve, sparsely set on rest of perinotum, intermingling with many minute ones; marginal spicules (Figures 7a, b) long, hyaline, smooth, 100–140 μm in length; hyponotum with numerous small papillae in anterior area; pallial fold much developed, deeply incised at posterior end, extending anteriorly as fingerlike projections; spicules of hyponotum (Figures 8a–d) rather sparse, slightly larger than those of perinotum, hyaline, smooth and blunt at tip, 50–60 μm in length; spicules on pallial fold (Figures 8e–g) minute, 35–45 μm in length and sparsely set; spicules on fingerlike projections (Figures 8h–j) slender, hyaline, pointed at tip, finely striated, 55–100 μm in length; papillae without spicules or, if present, exceedingly minute, shorter than 10 μm in length and very sparsely set (Figures 8k, l).

Radula (Figure 9): Central tooth (Figure 9b) oblong in outline, slightly dilated at middle of both sides, nearly straight at top with weak but entire cutting edge, basal portion constricted and thickened posteriorly on both sides with shallow concavity narrowing between these thickenings, prop plate with round end; centro-lateral (Figure 9c) with cusped edge at top, posterior portion strongly projecting and reflexed laterally, propped by basal plate with obtuse end; major lateral (Figure 9d) with strongly keeled shaft, dilated ventrally, curving dorsally with tridentate cusp, denticles short, almost equal in size, but middle one slightly larger than lateral ones; inner small lateral (Figure 9e) solid, much elevated, extended anteriorly at bottom; outer small lateral (Figure 9f) also elevated, roughly rhomboid-shaped and sinuate at posterior outer surface; major uncinus (Figure 9a) slender, spoon-shaped, shaft undulate twice with footlike basal plate anteriorly and narrow arched cusp of which length is longer than half length of shaft; inner and middle marginals thick and platelike; outer marginals thin and platelike.

Digestive tract (Figure 10): Stomach large, pouchlike, transversely constricted ventrally, light brown; blind end of stomach extended dorsally to right side of visceral mass, but not reaching dorsal surface; anterior intestine originating from left side of stomach, dorsally running posteriorly with U-shaped loop; intestinal valve directed anteriorly; tract of posterior intestine simple, revolving one and a half times, ventrally leading back to rectum.

Gills, gonopore, and nephridiopore: Gills holobranchial and abanal, originating from under the posterior margin of valve II extending to that of valve VI; gonopore and nephridiopore situated inside of posteriormost gill and behind same respectively.

Heart: Pericardium extending to the boundary between valves V and VI; heart with pair of auricular pores and pair of auriculo-ventricular ostia.

Coloration: Preserved valves whitish along jugum, uniformly dark brown on rest of tegmentum; interior of valves whitish, tinted with light greenish blue; perinotum uniformly light brown to brown; hyponotum light brown except for olivaceous anterior portion, often maculated with red when alive.

Remarks: This species was first described by PILSBRY (1893) based on a single specimen from Bering Island. The specimen was one of five specimens identified as *Placiphorella stimpsoni* by DALL (1886). Redescriptions were provided by BERRY (1917) and YAKOVLEVA (1952). Many differences exist between the holotype (USNM 106922) (Figure 48) and specimens identified by BERRY (1917) as *P. borealis* (USNM 215633) collected from a depth of 228 fathoms (ca. 417 m) off Shimshir Island, Kurile Islands. Berry's specimens have whitish valves, a narrower head valve, a smaller tail valve with the mucro situated at the posterior end, and a smooth perinotum. Judging from a comparison of the external morphology with the original description, the paratype of *P. uschakovi* Yakovleva, 1952 (CASIZ 019464) and locality records, Berry's specimens seem to be identical with *P. uschakovi*. The present species also resembles *P. **borealijaponica***, which is described in this paper as a new species (see **Remarks** under *P. **borealijaponica***).

Distribution: Bering Sea, Okhotsk Sea, Japan Sea, and Pacific Ocean from Bering Island to east coast of Hokkaido. Found on littoral and sublittoral zones of rocky shore.

Placiphorella ***borealijaponica*** Saito & Okutani, sp. nov.

(Figures 11–27, 49)

Placiphorella stimpsoni: ?DALL, 1886:210 (in part); PLATE, 1901:300–307, pl. 12, figs. 321–327; Is. TAKI, 1938: 350–355, pl. 14, figs. 13, 17, pl. 21, figs. 3, 7–9, pl. 22, figs. 7–15; 1954:26, pl. 11, figs. 5, 6; YAKOVLEVA, 1952: 76, fig. 36, pl. 5, fig. 4; ISHIKAWA, 1966:96. (All *non Chiton stimpsoni* Gould, 1859).

Materials examined: See Table 2.

Description: Body oval to broadly oval in outline, valves depressed, subcarinate, side slopes nearly straight; girdle widely extended anteriorly, uniformly olivaceous to light brown (Figures 11, 49).

Valves: Head valve (Figure 13) thick, stout, narrowly crescent-shaped, anterior slope straight to slightly concave with small roundish notch at apex, posterior margin of both sides slightly convex; tegmental surface without any sculpture except for concentric growth lines, but sometimes somewhat rough and wavy; posterior margin hardly raised; interior smooth, strongly thickened anteriorly; insertion plates short, thick, and weakly pectinate; slits usually 8, but occasionally up to 10 in number; slit rays inconspicuous.

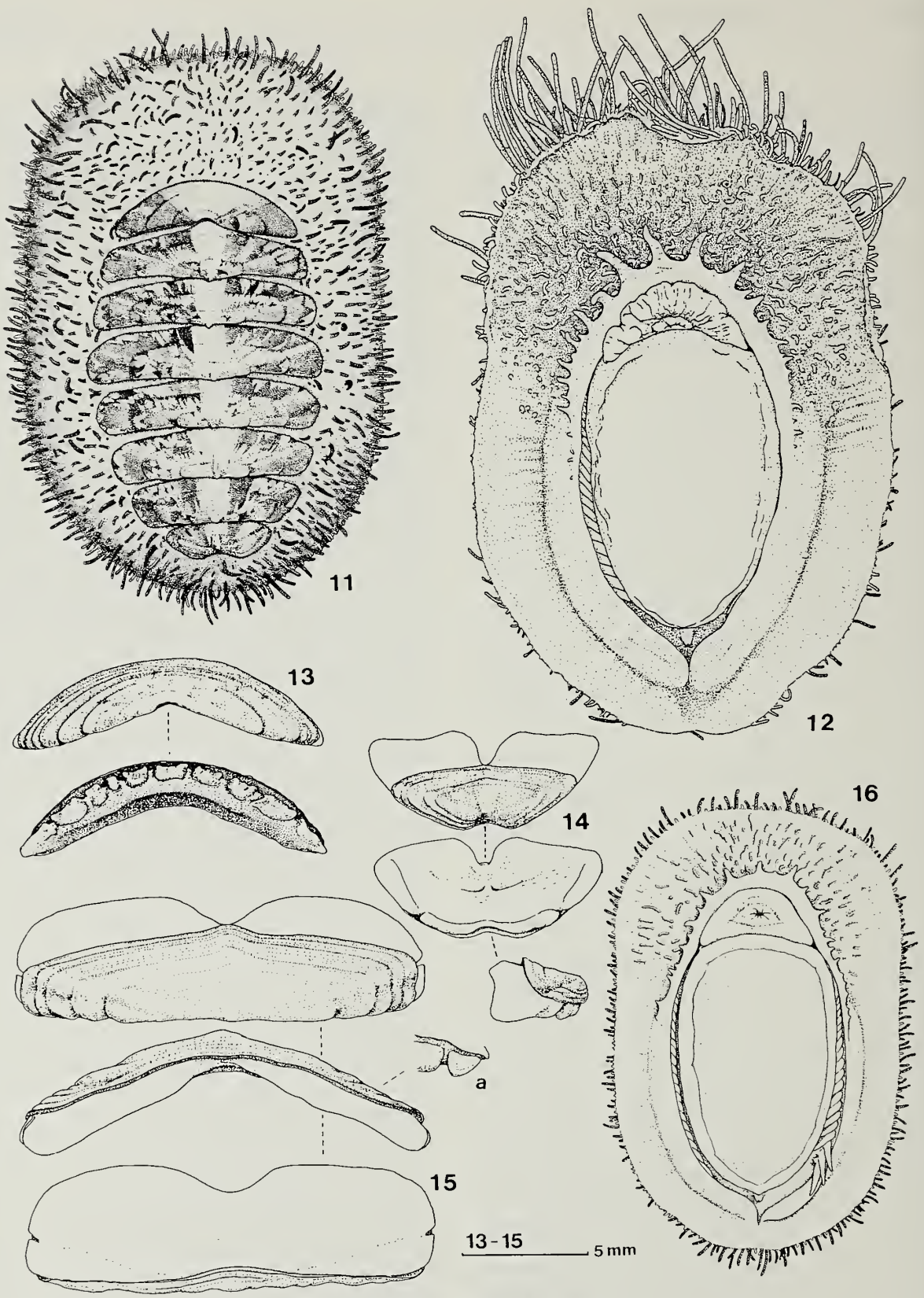
Intermediate valves (Figure 15) oblong in outline, much wider than long, widest at valve IV, subcarinate, not beaked posteriorly, having gently projecting false beak; lateral areas distinctly elevated with obsolete but wide diagonal and sutural ribs, both barely separable by shallow excavation; central area nearly smooth except for concentric growth lines; interior smooth with transverse callus, slightly convex anteriorly, extending from center to near slits; slit rays inconspicuous; sutural laminae very wide, thick, nearly straight and sharp at anterior edge, widely incised by jugal sinus, usually barely connected across jugum; insertion plates thick, short but usually extending beyond narrow eaves, obtuse at edge, slightly pectinate on lateral surface; insertion and sutural plates (Figure 15a) thickened, wedgelike on sides of slit.

Tail valve (Figure 14) small, depressed, roughly rhombic in shape, its greatest width including articulamentum decidedly shorter than tegmental width of head valve, and tegmental width slightly shorter than half width of those of valve IV: anterior margin of tegmentum regularly convex without false beak; mucro slightly raised, situated nearly at posterior end with shallow sinus; central area nearly smooth, slope slightly concave anterior to mucro; diagonal ribs raised, often roughened by growth lines, posterior area narrow; interior of valve callused posteriorly; sutural laminae broad, truncated anteriorly, separated by narrow sinus; insertion plates very short but clearly defined, posterior margin faintly roughened; one slit per side.

Girdle: Perinotum densely covered by minute, slender brownish orange spicules (Figures 18a, b) with deeply striated distal portion ending in a pointed tip, 30–50 μm in length; bristles on side of sutures (Figure 17) somewhat larger than others, smooth, composed of depressed, ellipsoidal, distally papillated, strongly striated, brownish orange spicules (Figure 17a), 100–150 μm in length, arranged in oblique series around axis and not imbricating each other; slightly smaller bristles closely set near anterior margin and posterior to tail valve, sparsely set on rest of perinotum, intermingling with many minute ones; marginal spicules (Figure 19) long, hyaline, nearly smooth, sharply pointed at tip, 130–200 μm in length; hyponotum with numerous small papillae that often coalesce to form a vermicular pattern in anterior region; pallial fold well developed, deeply incised at posterior end, extending anteriorly as fingerlike projections; spicules of hyponotum (Figures 20a–d) densely set, decidedly longer than those of perinotum, smooth, hyaline, blunt at tip, 80–120 μm in length; spicules on pallial fold (Figures 20e–g) slightly longer, attaining 160 μm in length; fingerlike projections also with hyaline spicules (Figures 20h, i), of which shape almost same as those on perinotum; spicules on papillae (Figure 20j) minute, hyaline, finely striated, 20–30 μm in length and sparsely set.

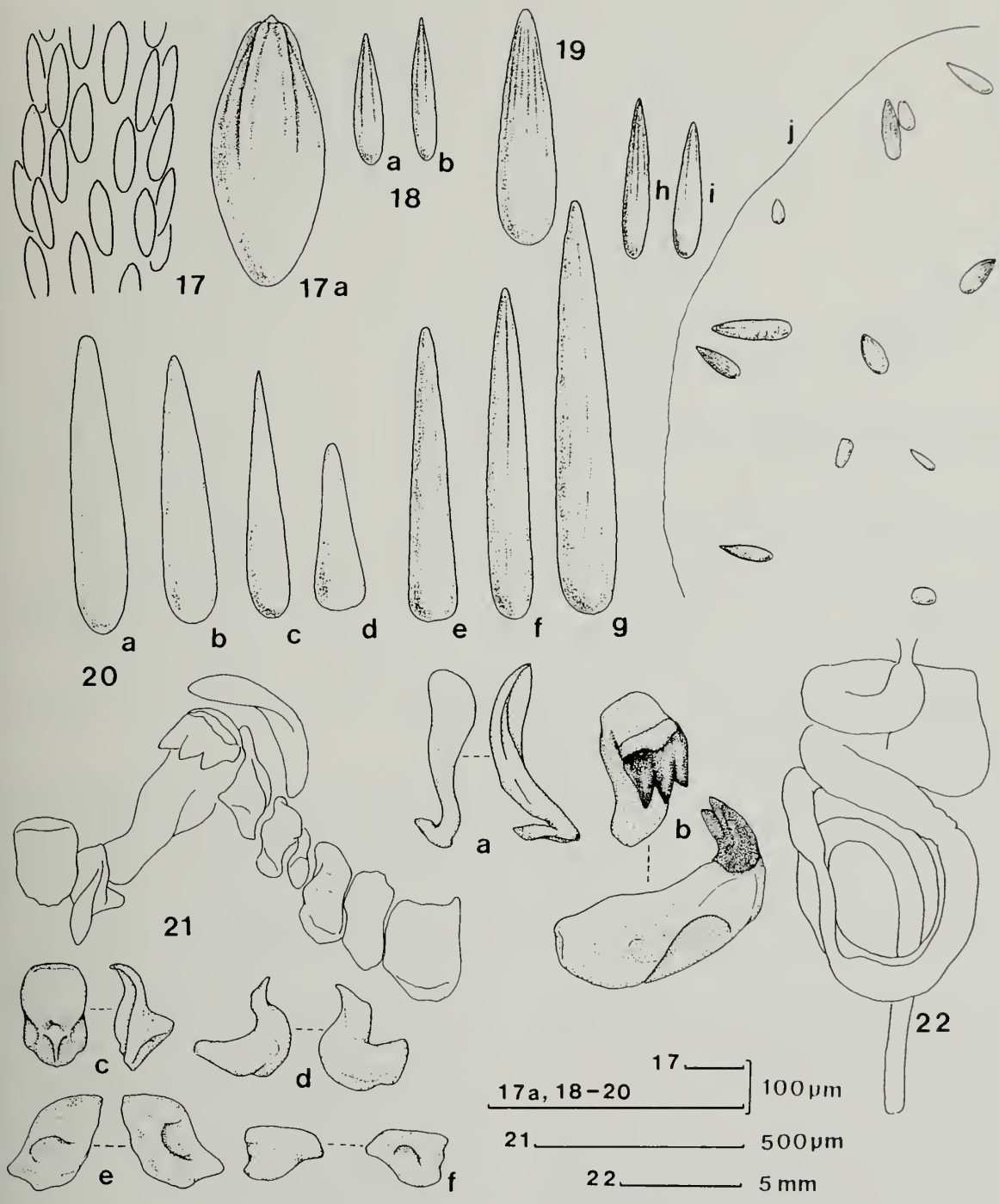
Radula (Figure 21): Central tooth (Figure 21c) oblong in outline, slightly sinuate at the middle on both sides, gently arched at top with entire cutting edge, basal portion abruptly constricted and thickened posteriorly on both sides with a shallow concavity narrowing between these thickenings, small projection sometimes present between these thickenings, then basal part of posterior end becoming trilobed, prop plate thick with round end; centro-lateral (Figure 21d) with dorsal edge ascending to lateral corner which is slightly thickened and reflexed as small cusp, posterior portion thickened, concaved laterally, forming an auricular projection, basal plate truncated laterally; major lateral (Figure 21b) with strongly keeled shaft, dilated ventrally, curving dorsally with tridentate cusp; denticles are nearly equal in size but middle one slightly larger than lateral ones; inner small lateral (Figure 21e) solid, much elevated, bottom wider than top, narrowly elongate anteriorly; outer small lateral (Figure 21f) also elevated, roughly rhomboid-shaped, roundly sinuate at posterior outer surface; major uncinus (Figure 21a) spoon-shaped, shaft undulated twice with footlike basal plate and arched cusp of which length is longer than half length of shaft; inner and middle marginal thick, platelike, often with small pore basally; outer marginal large, thin, platelike.

Digestive tract (Figure 22): Stomach large, pouchlike, transversely constricted ventrally, light grayish brown; blind end of stomach extended dorsally to right side of visceral mass, but not reaching dorsal surface; anterior intestine originating from left side of stomach, running posteriorly with U-shaped loop; intestinal valve directed anteriorly; tract of posterior intestine simple, revolving one and a half times ventrally, leading back to rectum.



Explanation of Figures 11 to 16

Figures 11–16. *Placiphorella* ***borealijaponica*** Saito & Okutani, sp. nov. Figures 11, 16: paratype 4; Figure 12, paratype 3; Figures 13–15, paratype 5. Figure 11: dorsal view of animal. Figure 12: ventral view of animal. Figure 13: head valve, dorsal and ventral views. Figure 14: tail valve, dorsal, ventral, and lateral views. Figure 15: valve IV, dorsal, anterior, and ventral views. Figure 15a: valve IV, lateral portion. Figure 16: ventral view of animal.



Explanation of Figures 17 to 22

Figures 17–22. *Placiphorella* ***borealijaponica*** sp. nov. Figures 17–22: paratype 2; Figure 21, paratype 1. Figure 17: bristle, arrangement of spicules. Figure 17a: spicule of bristle. Figures 18a, b: spicules on perinotum. Figure 19: marginal spicule. Figures 20a–d: spicules on hyponotum. Figures 20e–g: spicules on pallial fold. Figures 20h, i: spicules on fingerlike projection. Figure 20j: spicules on papilla. Figure 21: half radula row (major uncinus is removed except for basal plate and major uncinus of a row immediately anterior is shown). Figure 21a: major uncinus, posterior and inner lateral view. Figure 21b: major lateral, anterior and outer lateral views. Figure 21c: central, anterior and lateral views. Figure 21d: centro-lateral, both lateral views. Figure 21e: inner small lateral, both lateral views. Figure 21f: outer small lateral, both lateral views. Figure 22: digestive tract, dorsal view.

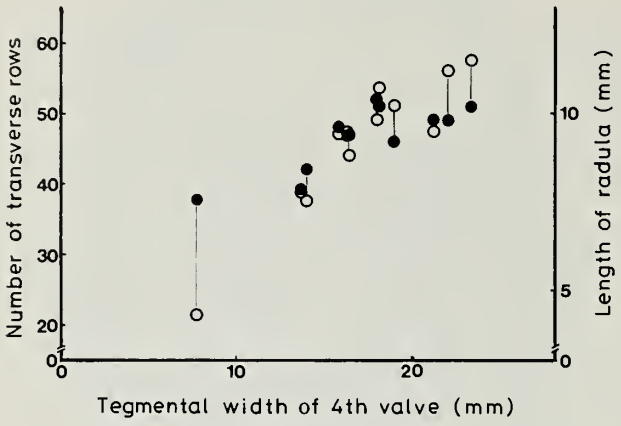


Figure 23

Relationship between width of valve IV and radula. Open circles, length; solid circles, number of transverse rows (n = 12).

Gills, gonopore, and nephridiopore: Gills holobranchial and abanal, originating at posterior margin of valve II to that of valve VI; gonopore and nephridiopore situated between inside of two posteriormost gills and posterior to last gill respectively.

Heart: Pericardium extending to the boundary between valves V and VI; heart with pair of auricular pores and pair of auriculo-ventricular ostia.

Coloration: In preserved condition, valves whitish along jugum, uniformly brown or brown with white and blue streaks on rest of tegmentum; interior of valves light blue, often tinted with brown on insertion plate of head valve; perinotum uniformly olivaceous to light brown; hyponotum light brown.

Ontogenetic variations: No marked changes in morphological characters present in body length from 12 to 47 mm. Transverse rows of radula gradually increase with growth (Figure 23).

Type locality: Hamamasu, Hokkaido.

Type depository: Holotype in NSMT Mo-64663, paratypes 1 to 4 in NSMT Mo-64664 to Mo-64667, paratypes 5 and 6 in USNM 859353 and 859354, paratypes 7 and 8 in CASIZ 066636 and 066637.

Remarks: Owing to similar general appearance, the present species has long been confused with *Placiphorella stimpsoni* (Gould, 1859). The type specimen of *P. stimpsoni* was collected from "Hakodadi Bay" (Hakodate Bay). DALL (1925) established a new genus *Langfordiella* based on his species *L. japonica* collected from "Emi Bashiu" (Emi, Chiba Prefecture). TAKI (1938) ignored the genus *Langfordiella* and considered *L. japonica* to be identical with his *P.* "*stimpsoni*" collected from Mutsu Bay, but later he (1954) separated them into two species.

An examination of the type specimens of *Chiton* (*Molpalia*) *stimpsoni* Gould, 1859 (USNM 1646) (Figure 50)

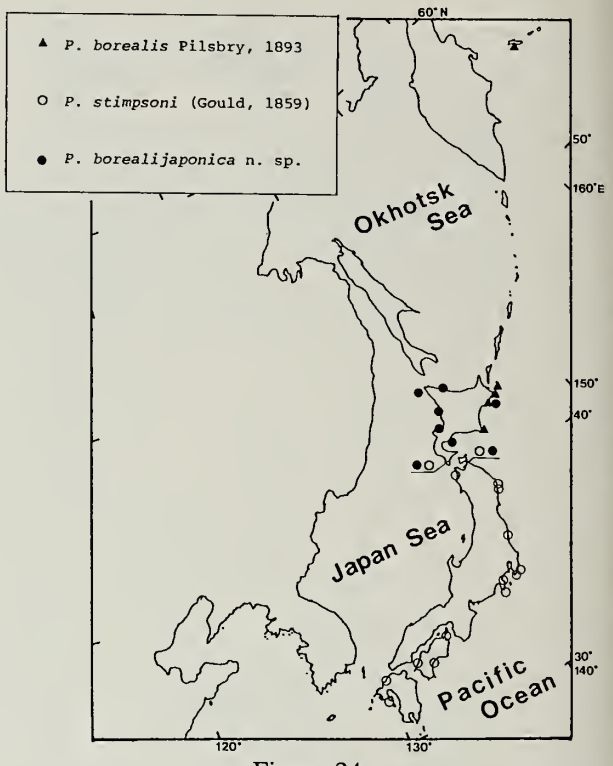


Figure 24

Distribution of the three species of *Placiphorella* examined in this study.

and *Langfordiella japonica* Dall, 1925 (USNM 333541; see Figure 52) as well as 93 specimens collected from various Japanese localities, indicates that *Placiphorella stimpsoni* (Gould, 1859) and *P. japonica* (Dall, 1925) are conspecific, but *P.* "*stimpsoni*" *sensu* TAKI (1938, 1954) is a different species which is here described as a new species. One reason for past confusion may be that *P. stimpsoni* and *P.* ***borealijaponica*** sp. nov. are sympatric around the Tsugaru Strait (Figure 24). South of the southern tip of Hokkaido one finds *P. stimpsoni* while *P.* ***borealijaponica*** occurs to the north of the northern tip of Honshu. Differences between these two species include: the shape of the tail valve, insertion plate of the head valve, spicules of the bristles, and color of the perinotum. Spicules of the bristles of the two species are different not only in shape but also in size (Figure 25). *Placiphorella* ***borealijaponica*** also closely resembles *P. borealis* but is separable by morphological differences of the head and tail valve and spicules on the hyponotum. Ratios of articulamental width of the tail valve to tegmental width of the head valve are considerably different between these two species (Figure 26). Other differences between the three species are summarized in Figure 27.

Some anatomical features of the soft parts of these three species were also compared. Although no distinct feature

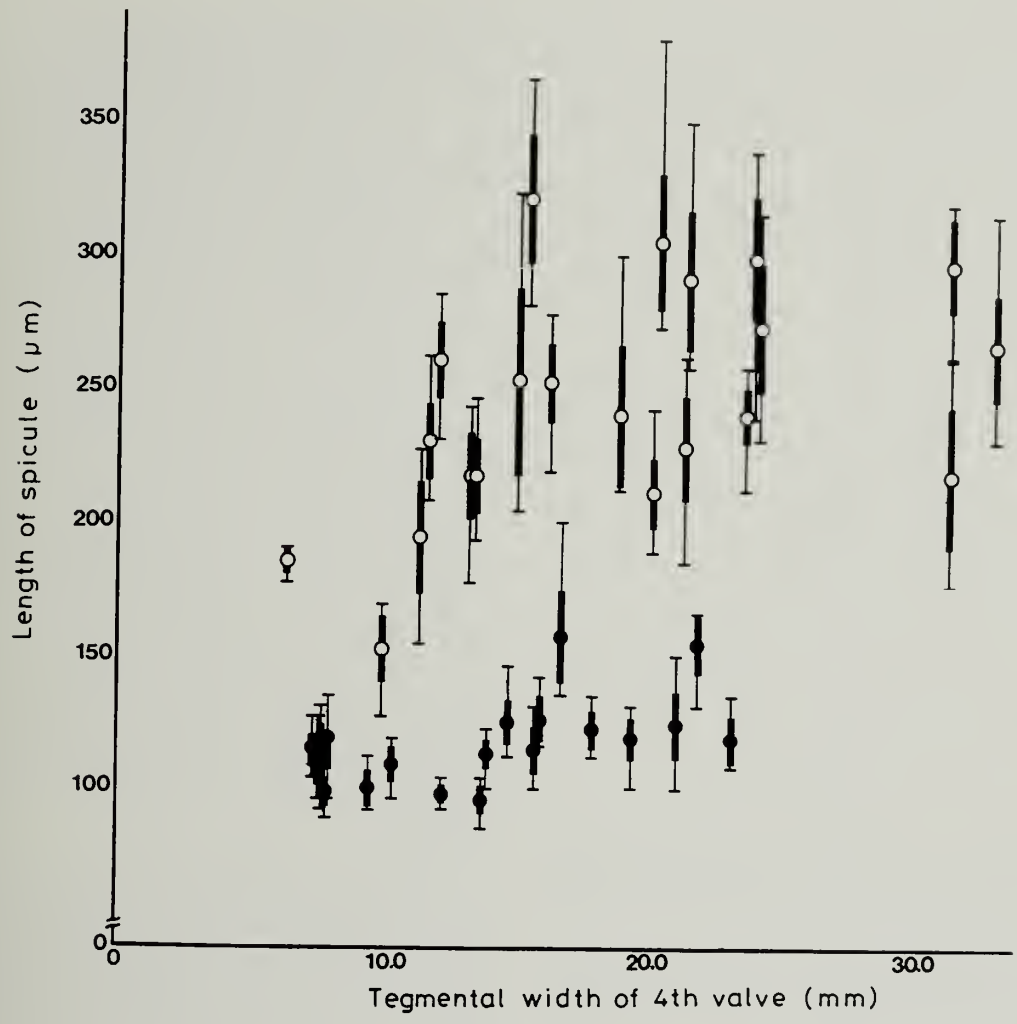


Figure 25

Relationship between tegmental width of valve IV and length of spicule on bristles in two *Placiphorella* species. Vertical solid bars, standard deviation; lines, range. Open circles, mean for *P. stimpsoni*; solid circles, mean for *P. **borealijaponica***.

could be used to distinguish one from another, several facts were noteworthy.

The general looping pattern of the digestive tract is almost the same among all three species; however, it is slightly more complicated in *Placiphorella stimpsoni* than in the others. This pattern is stable even when the gut is pressed by the mature gonad.

The nephridiopore is situated posterior to the posteriormost gill in all three species. According to Pelseneer (1898, *fide* HYMAN, 1967) and PLATE (1901), the nephridiopore of most species that have abanal gills is situated anterior to the posteriormost gill. Plate noted that *Tonicella marmorea*, which has the nephridiopore situated posterior to the posteriormost gill, is the only exception.

The auriculo-ventricular ostia are found in a single pair in all three species. This state is considered to represent a rather primitive condition, because Lepidopleuridae and Ischnochitonidae have only a single pair of auriculo-ventricular ostia besides selected species of the Mopaliidae, namely, *Mopalia muscosa*, *M. wosnessenski*, *Amicula pallasi*, and *Katharina tunicata* (PLATE, 1901).

Distribution: Northern part of Honshu and Hokkaido, northwestern part of Pacific Ocean, Okhotsk Sea, northern part of Japan Sea. Found on rocks or under large stones in the littoral and sublittoral zones.

Placiphorella stimpsoni (Gould, 1859)

(Figures 28–46, 50–52)

Chiton (*Molpalia*) [*sic*] *stimpsoni* GOULD, 1859:165; 1862: 118 (*fide* TAKI, 1938); JOHNSON, 1964:153.

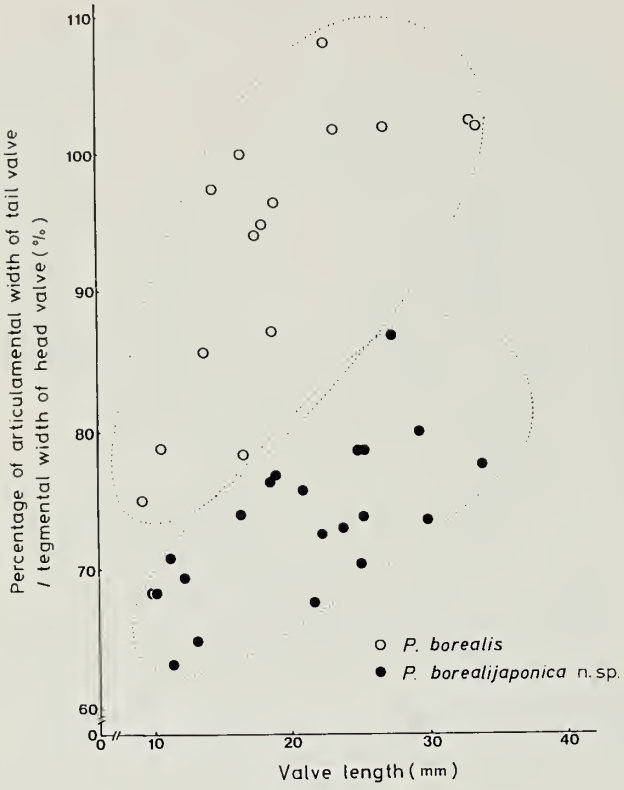


Figure 26

Relationship between valve length and percentage of articulamental width of tail valve divided by tegmental width of head valve of *Placiphorella borealis* and *P. **borealijaponica***.

Placiphorella stimpsoni: PILSBRY, 1893:307–309, pl. 62, figs. 84–87; BERRY, 1917:12–13, pl. 8, figs. 1, 2, pl. 9, figs. 1–8; LELOUP, 1942:13, fig. 5.
Placiphorella sp.: IS. TAKI, 1924:286–287, 1 text-fig.
Langfordiella japonica DALL, 1925:96; THIELE, 1929:11.
Placiphorella japonica: IS. TAKI, 1954:24–26, pl. 11, figs. 3, 4, pl. 12, figs. 4, 5, pl. 13, figs. 6–9, pl. 14, figs. 5–8, pl. 15, figs. 1, 2, 7; ISHIKAWA, 1966:96, pl. 1, fig. 10.

Materials examined: See Table 4.

Description: Body broadly oval in outline; valves depressed, subcarinate, side slopes nearly straight; girdle broadly extended anteriorly, dark bands on light colored background (Figures 28, 51).

Valves: Head valve (Figures 29, 30, 32) thick, stout, wide, crescent-shaped, anterior slope straight to slightly convex, with shallow roundish notch at apex, posterior margin of both sides slightly convex; tegmental surface without any sculpture except for concentric growth lines, posterior margin barely raised; interior smooth, strongly thickened anteriorly; insertion plates short, exceedingly thick and deeply pectinate, occasionally with minute, irregularly arranged accessory denticles anteriorly (Figure 30a); usually 8 slits but occasionally up to 12; slit rays corresponding to slits but not grooved, provided with several minute pores.

Intermediate valves (Figures 31, 35) oblong in outline, much wider than long, widest at valve IV, subcarinate, not beaked posteriorly, having small but usually sharply projecting false beak; lateral areas distinct, elevated, with inconspicuous but wide diagonal and sutural ribs, shallowly excavated in between; central area nearly smooth; interior smooth with transverse callus slightly convex anteriorly, extending from center to near slits; slit rays indistinctly grooved; slit narrow, one on each side; sutural laminae very wide, nearly straight and sharp at anterior edge, shallowly and widely incised by jugal sinus, but usually connected across jugum by narrow lamina; insertion plates thick, short, usually not extending beyond narrow eaves, obtuse at edge, pectinate on outer surface.

Tail valve (Figure 34) small, depressed, roughly widely triangular in outline, its greatest width including articulamentum decidedly shorter than tegmental width of head valve; anterior edge slightly convex, often lacking small false beak; posterior margin bordered by raised diagonal ribs, slightly sinuate at posterior end; posterior area narrow, lying beneath diagonal ribs; central area nearly smooth, slope slightly concave anterior to mucro; interior heavily callused posteriorly; slit poorly developed but sometimes obsolete or lacking in older animals; sutural laminae broad, truncated at anterior edge, narrowly and deeply incised by jugal sinus, but usually connected to each other across jugum.

Girdle: Perinotum beset with minute, hyaline, drop-shaped spicules (Figures 41a–c), 35–55 μm in length, often with bubblelike structure internally; bristles on sutures (Figure 39) large, smooth, composed of long spicules (Figures 39a–d) arranged in oblique series around axis and imbricating each other; spicules striated, papillated at tip, brown or olive green, 200–350 μm in length; slightly smaller bristles closely set near anterior margin and posterior to tail valve; smallest ones closely set around margin, sparsely set on rest of perinotum; marginal spicules (Figures 40a, b) long, hyaline, sharply pointed at tip, distal two-thirds finely striated, 120–140 μm in length; hyponotum with numerous small papillae often coalescing to form a vermiculation in anterior portion, having well developed pallial fold deeply incised at posterior end, extending anteriorly as fingerlike projections; spicules of hyponotum (Figures 42a–c) densely set, decidedly larger than those on perinotum, hyaline, smooth, blunt at tip, 100–135 μm in length; spicules on pallial fold (Figures 42d–g) slightly longer and more slender; papillae sparsely set with small, hyaline, smooth spines (Figure 42j), 30–50 μm in length.

Radula (Figure 43): Central tooth oblong in outline, nearly straight on both sides having strong and entire cutting edge at top, abruptly constricted and thickened posteriorly on both sides of basal portion where concavity narrows, prop plate triangular with simple round end; centro-lateral slightly thickened at lateral corner of top, projecting and thickened posteriorly, curving dorsally

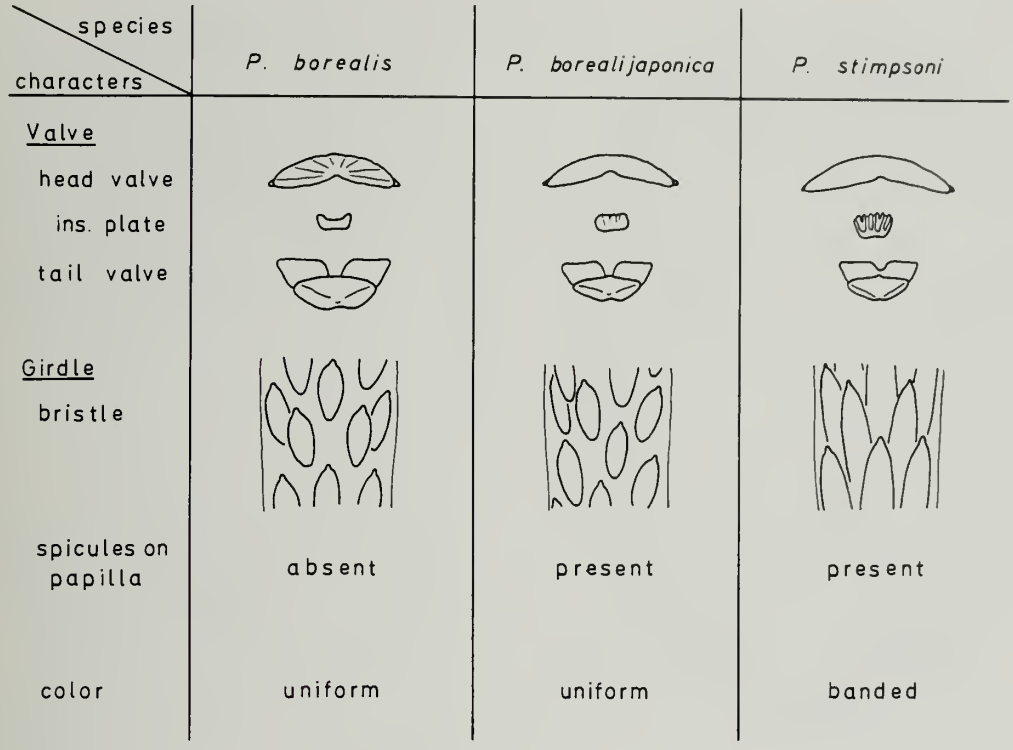


Figure 27

Distinctions among the three species of *Placiphorella*.

forming auriculate projection, basal plate with truncate end; major lateral with strongly keeled shaft, dilated ventrally, curving upward anteriorly with tridentate cusp; denticles nearly equal in size, but middle one slightly longer than others; inner small lateral solid, much elevated posteriorly, bottom wider than top, narrowly elongated anteriorly; outer small lateral also elevated, rhomboid-shaped, sinuate at posterolateral surface; major uncinus slightly curved with narrow cusp of which length is about half length of shaft; inner and middle marginals rhombic

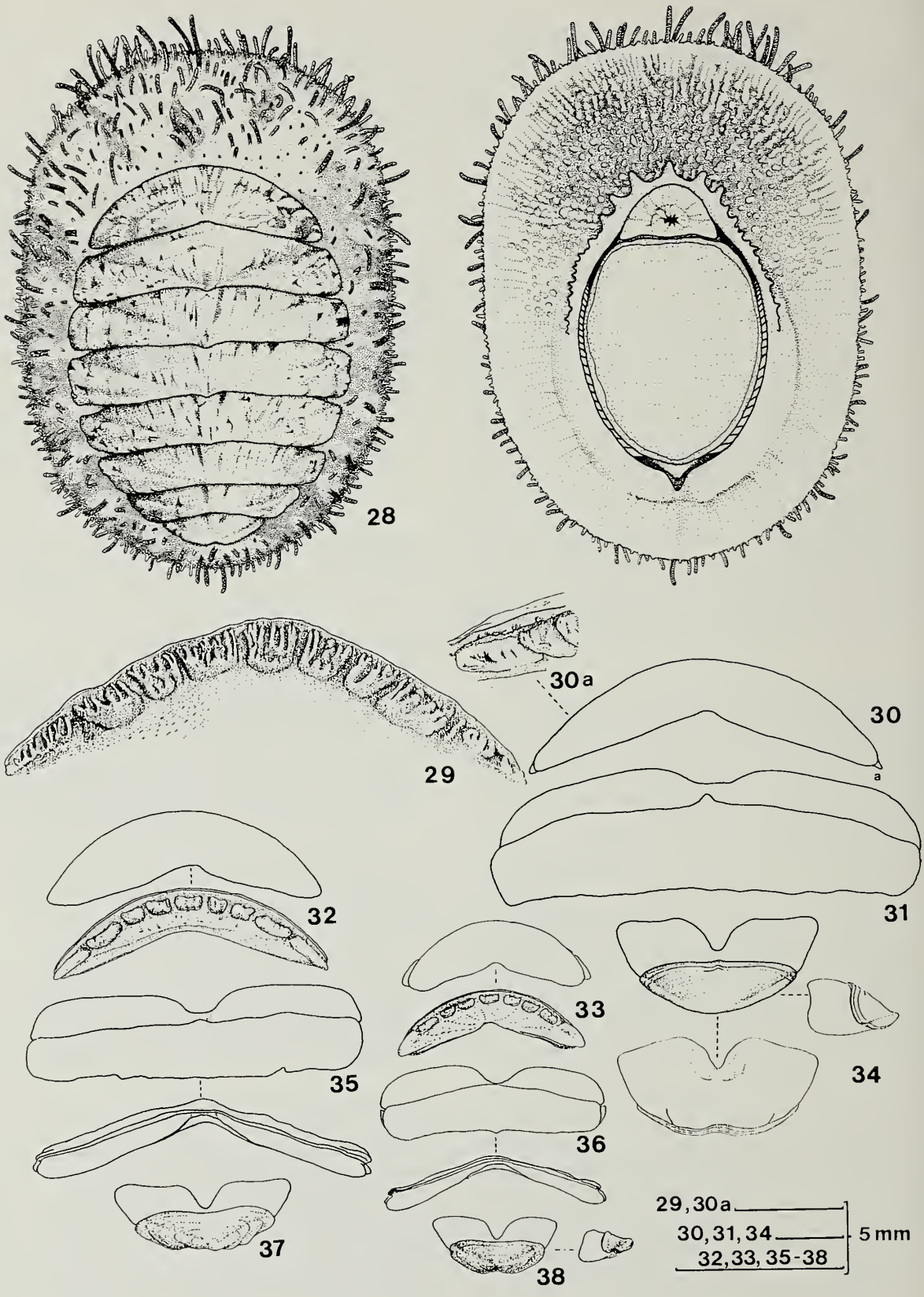
→

Explanation of Figures 28 to 38

Figures 28–38. *Placiphorella stimpsoni* (Gould, 1859). Figure 28: valve length 31.9 mm, from Manazuru; Figure 29: valve length 35.0 mm, from Emi, USNM 333541 (one of the syntypes of *Langfordiella japonica*); Figures 30, 31, 34: valve length 33.2 mm, from Shimoda; Figures 32, 35, 37: valve length 12.6 mm, from Yokonami Pen.; Figures 33, 36, 38: valve length 9.3 mm, from Banda. Figure 28: dorsal and ventral view of animal. Figure 29: insertion plates of head valve. Figure 30: head valve, outline of dorsal view. Figure 30a: insertion plates and accessory denticles. Figure 31: valve IV, outline of dorsal view. Figure 32: head valve, outline of dorsal view and ventral views. Figure 33: head valve, outline of dorsal view and ventral views. Figure 34: tail valve, dorsal, ventral, and lateral views. Figures 35, 36: valve IV, outline of dorsal and anterior views. Figure 37: tail valve, dorsal view. Figure 38: tail valve, dorsal and lateral views.

Explanation of Figures 39 to 44

Figures 39–44. *Placiphorella stimpsoni* (Gould, 1859). Figure 39a: valve length 18.2 mm, from Ozuchi; Figure 39b: valve length 31.5 mm, from Sumoto; Figure 39c: valve length 15.3 mm, from Ozuchi; Figure 39d: valve length 12.6 mm, from Yokonami Pen.; Figures 40–42: valve length 31.9 mm, from Manazuru Pen.; Figures 43, 44c: valve length 33.2 mm, from Shimoda; Figure 44a: valve length 9.3 mm, from Banda; Figure 44b: valve length 24.8 mm, from Banda. Figure 39: bristle, arrangement of spicules. Figures 39a–d: spicules of bristle. Figures 40a, b: marginal spicules. Figures 41a–c: spicules on perinotum. Figures 42a–c: spicules on hyponotum. Figures 42d–g: spicules on pallial fold. Figures 42h, i: spicules on fingerlike projection. Figures 42j: spicules on papilla. Figure 43: half radula row (major uncinus is removed except for basal plate and major uncinus of a row immediately anterior is shown). Figures 44a–c: digestive tract, dorsal view.


28
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32, 33, 35-38
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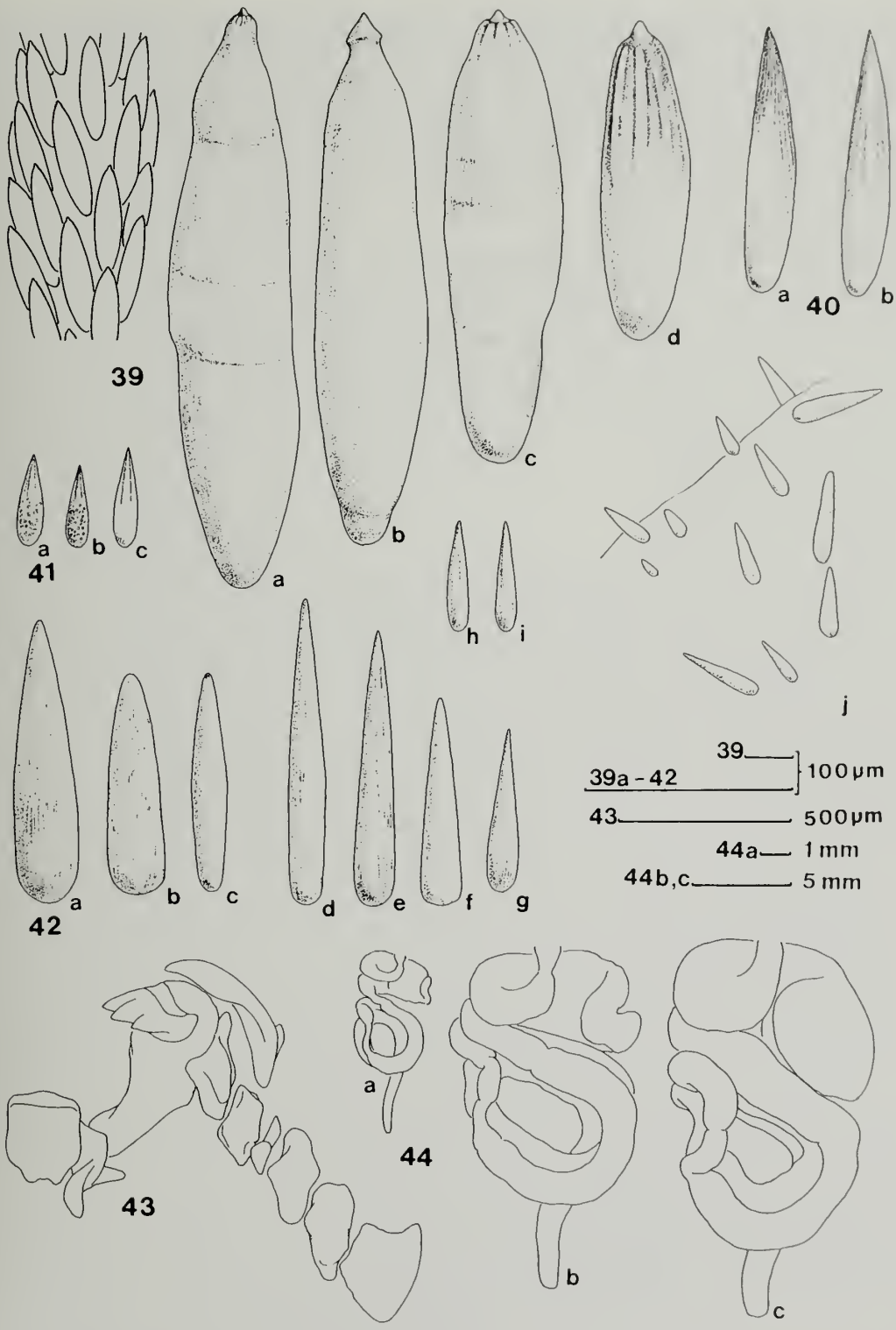
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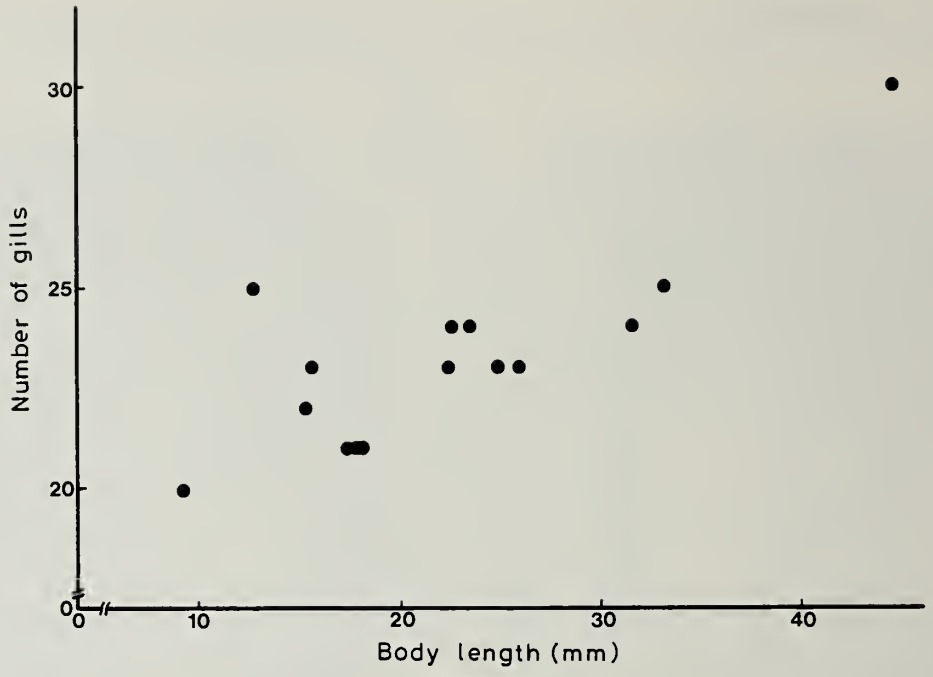


Figure 45

Relationship between body length and number of gills (n = 15).

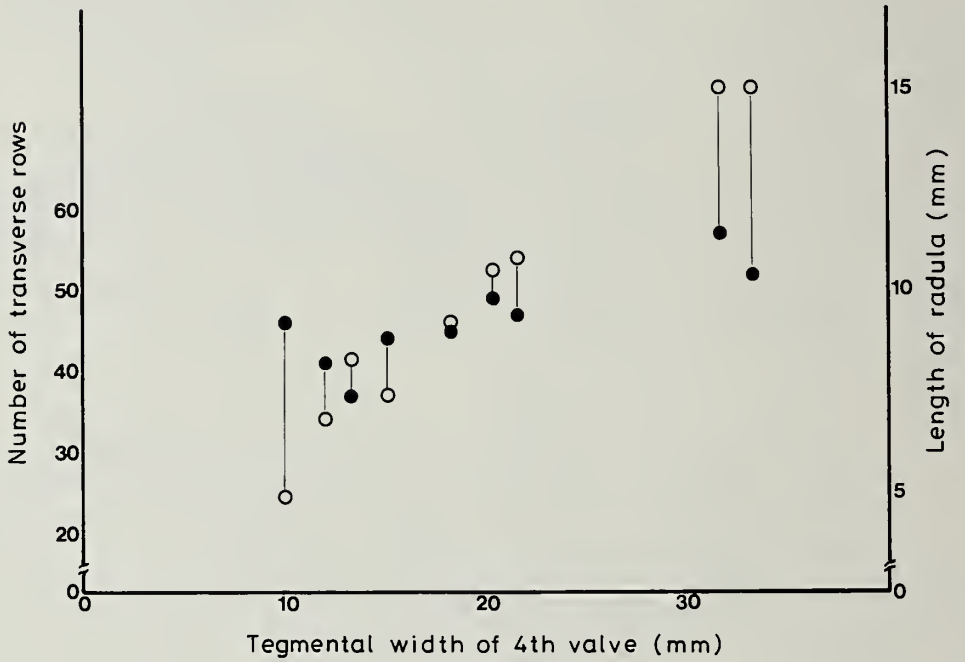


Figure 46

Relationship between width of valve IV and radula. Open circles, length; solid circles, number of transverse rows (n = 9).

→

Explanation of Figures 47 to 52

Figure 47. *Placiphorella borealis* Pilsbry, 1893. Holotype (USNM 106922). Width of head valve 15 mm.

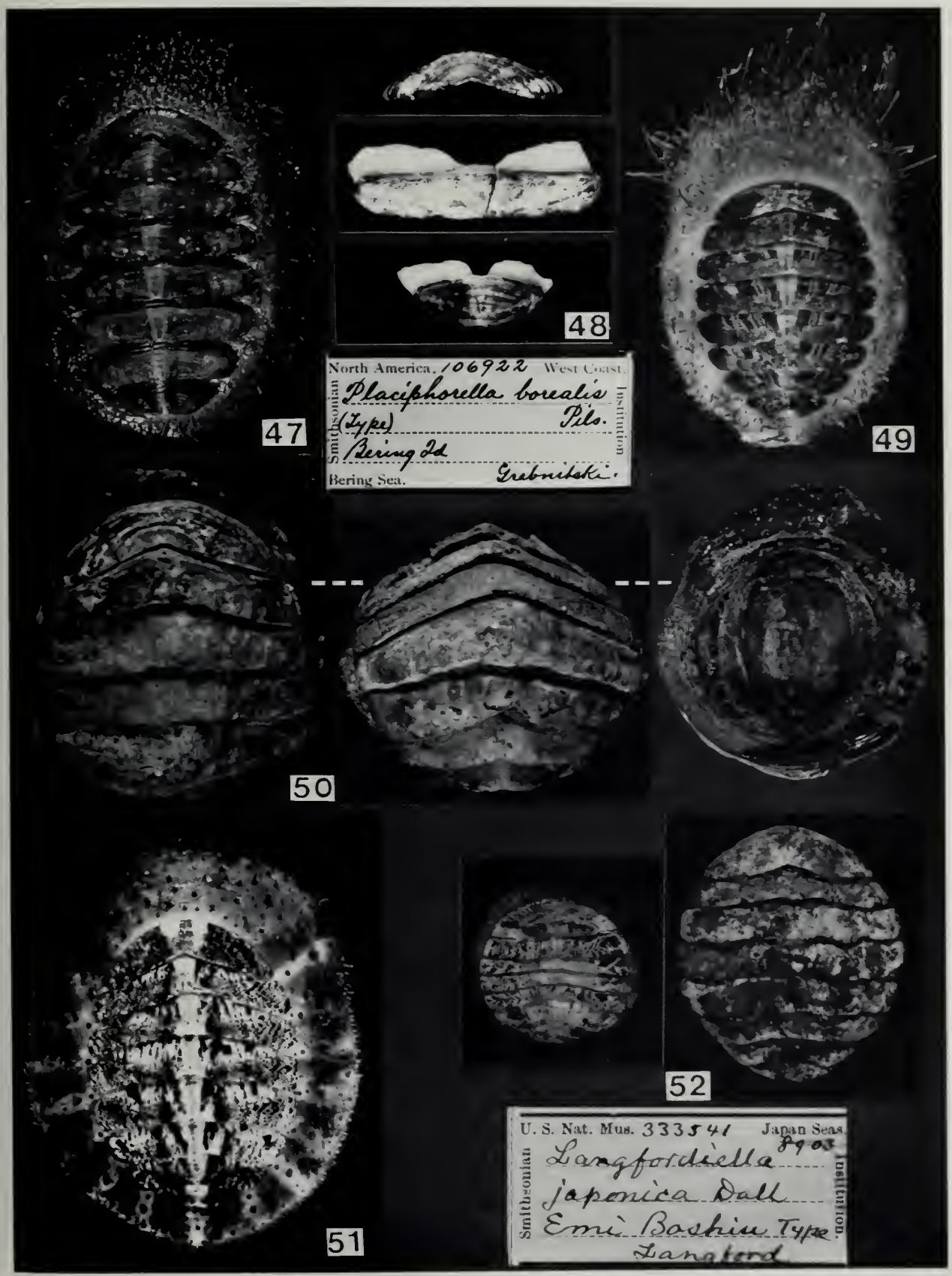
Figure 48. *Placiphorella borealis* Pilsbry, 1893. Approximate body length 45 mm (valve length 33.8 mm), from Nosappu, Hokkaido.

Figure 49. *Placiphorella* ***borealijaponica*** Saito & Okutani, sp. nov. Paratype 3.

Figure 50. *Chiton* (*Molpalia*) *stimpsoni* Gould, 1859. One of two syntypes (USNM 1646). Valve length 24.5 mm.

Figure 51. *Placiphorella stimpsoni* (Gould, 1859). Approximate body length 50 mm (valve length 33.4 mm), from Shimoda.

Figure 52. *Langfordiella japonica* Dall, 1925. Syntypes (USNM 333541). Valve length 35.0 mm and 20.3 mm respectively.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49
50
51
52
North America. 106922 West Coast.
Smithsonian Placiphorella borealis Institution
(Type) Pils.
Bering 2d
Bering Sea. Grebnitski.
U. S. Nat. Mus. 333541 Japan Seas
Smithsonian Langfordiella 89 03 Institution
japonica Dall
Emi Boshin Type
Langford

in shape, thick, and platelike, and outer marginal large, thin, and platelike.

Digestive tract (Figure 44c): Stomach large, pouchlike, but appearing as double tube because of strong mesial constriction, light greenish brown; blind end of stomach extending dorsally to right side of dorsal surface of visceral mass; anterior intestine originating from left side of stomach, running posteriorly with U-shaped loop; intestinal valve directed inward; tract of posterior intestine simple, revolving one and a half times, ventrally leading back to rectum.

Heart: Anterior end of pericardium extending to the boundary between valves V and VI; heart with pair of auricular pores and pair of auriculo-ventricular ostia.

Gill: Holobranchial and abanal, number gradually increasing with growth (Figure 45); gonopore and nephridiopore situated between inside of two posteriormost gills and immediately behind posteriormost gill respectively.

Coloration: Preserved valves usually whitish, irregularly spotted or streaked with pink, brown, blue-green, and black; interior of valves uniformly white or tinted with blue-green; perinotum creamy yellow to light brown, with blackish bands; hyponotum uniformly creamy yellow to light brown, but anterior portion of both surfaces often maculated with red when alive.

Infraspecific and ontogenetic variations: Outline of valves generally slender in young individuals but roundish in adults. However, shape variable in adults; ratio of valve length to tegmentum width of valve IV ranging from 1.0 to 1.5; width sometimes wider than length (USNM 333541).

Head valve: Insertion plates already thickened in individual of 9.3 mm valve length, but pectination weak (Figure 33). In older animals, as pointed out by Taki (1954), insertion plate strongly pectinate (Figure 29) sometimes with accessory denticles anteriorly (Figure 30a).

Intermediate valves: Insertion plate of intermediate valves more pectinate with growth. Usually, in young individuals, sutural laminae barely connected to each other across jugal area (Figure 36), but well connected in full-grown adults (Figure 31). In adolescent or medium-sized individuals, sutural laminae sometimes separated by jugal sinus.

Tail valve: Allometric growth of tail valve remarkable (Taki, 1954).

Radula: Ratio of radula length to valve length almost constant from young individuals to full-grown adults and number of transverse rows gradually increases with growth (Figure 46).

Digestive tract: Blind end of stomach in young individuals (Figure 44a), situated in middle of right surface of visceral mass, intestinal valve runs anteriorly. As animal grows, blind end of stomach extends dorsally (Figure 44b), and turns dorsally to left side (Figure 44c), while intestinal valve turns inwardly.

Remarks: According to Johnson (1964), the holotype specimen of *Chiton stimpsoni* is USNM 1646. However, we found that two specimens are contained in the lot with this number. Both specimens are dried and intact animals, and they are decidedly conspecific. One that looks older than the other has written directly on hyponotum the number 1646; its valve length is 24.5 mm (Figure 50). The other specimen is accompanied by a paper label with the same number, and its valve length is 18.6 mm. In the original description, Gould said "length 1.5 poll." (=38.1 mm). Judging from the valve length, the larger one probably corresponds to Gould's specimen. Johnson (1964) thought the specimen that had been described and figured by Pilsbry (1893:308, pl. 63, figs. 85, 86, 88) was the holotype, although Pilsbry gave "length 17 mm" as the measurement of the "type of USNM 1646." Pilsbry's specimen may correspond to the smaller one, if Pilsbry's "length" means valve length. Furthermore, our observation of the specimens revealed no trace of disarticulation at the hands of Pilsbry, although he had described every character of the articulamenta of the valves. From the above-mentioned facts, it is not conclusive at present if either of these two specimens should be regarded as the holotype. Therefore, it is safe to treat them as the syntype in this paper.

Placiphorella stimpsoni has been long confused with *P. **borealijaponica*** sp. nov. (see **Remarks** under that species). *Placiphorella velata* (Carpenter MS) Dall, 1879, also closely resembles this species by its vivid coloration of the valves and girdle, and the exceedingly thick and pectinate insertion plate of the head valve. The two species are sufficiently separable by the shape of the tail valve, especially the posterior area, and the spicules of the bristles. Both species are distributed on both sides of the North Pacific and the southern distribution of each species extends to about 30°N. It is interesting that these two related forms are allopatrically distributed on both sides of the North Pacific.

Wu & Okutani (1985) recorded *Placiphorella "stimpsoni"* from a depth of 1210–1235 m off Mikura Island, Izu Islands, but re-examination of the specimen (NSMT Mo-60008) revealed that it is a quite different species, *Placiphorella* sp., which is closely related to the northeastern Pacific deep-water species *P. pacifica* Berry, 1919.

Distribution: Pacific coast of Japan, Japan Sea, and East China Sea, from southern part of Hokkaido to Kyushu. Found on littoral and sublittoral zones of rocky shores.

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NOTES, INFORMATION & NEWS

Field Observations on Feeding and Antagonistic Behavior by *Pteraeolidia ianthina* (Nudibranchia: Aeolidoidea)

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Feeding

On 19 March 1982, I observed an 85-mm specimen of *Pteraeolidia ianthina* eating hydranths of the athecate hydroid *Halocordyle distica* (Goldfuss) at a depth of 9 m on the northwestern side of Pelorous Island, northern Queensland, Australia. This fortuitous observation formed the basis for a previous statement that this aeolid fed on hydroids (WILLAN & COLEMAN, 1984).

On 1 December 1985, Messrs. R. McGill and D. Firman observed a specimen about 50 mm long consume a hydranth of *Ralpharia magnifica* Watson at a depth of 6 m on the northern side of Muttonbird Island, Coffs Harbour, northern New South Wales, Australia. According to their recollections, these divers watched one *Pteraeolidia ianthina* from a group of four crawl towards a solitary *R. magnifica*. This approach lasted some 15 min, during which time the animal crawled approximately 15 cm. Upon reaching the base of the hydroid, the *P. ianthina* proceeded to climb its hydrocaulus (a height of 2.5 to 3 cm; *R. magnifica* is an exceptionally large tubulariid hydroid), a behavior lasting a further 10 min. At the top, the nudibranch briefly arched the anterior 2 to 3 cm of its body away from the hydranth. Then it made a sudden lunge forwards and, after initially grasping some aboral tentacles, rapidly devoured the whole hydranth. The hydranth was consumed in less than 1 min. The *P. ianthina* did not eat the hydrocaulus, but returned to the substratum once it had fed. A further dive on the same site two weeks later revealed all the *Ralpharia* hydranths surrounding the one eaten by the *P. ianthina* had also been consumed.

On 30 August 1986, these same divers observed another feeding attack by *Pteraeolidia ianthina* at a depth of 10 m on the southern side of Split Solitary Island near Coffs Harbour. This time, however, they had deliberately placed a 60-mm *P. ianthina* near the base of a *Ralpharia magnifica* individual. The *P. ianthina* fed as before, but this time it bent the hydrocaulus into a right angle as it fed from the substratum. During this episode, which lasted approximately 2 min, Mr. McGill took two photographs, one of which is reproduced here (Figure 1). It shows the *P. ianthina* actually devouring the hydranth. Note the nudibranch's outstretched oral tentacles as well as its backwardly contracted rhinophores.

Antagonistic Behavior

On 28 January 1988, Dr. T. M. Gosliner and I witnessed an aggressive encounter between two adult (approximately 60 mm long) *Pteraeolidia ianthina* at 5 m on the summit of "Planet Rock," an isolated sheer-walled pinnacle in Astrolabe Bay on the northern coast of Papua New Guinea. We watched for 10 min as two animals engaged each other in what appeared to me to be a fighting bout. Each animal flailed the anterior third of its body against the opponent, biting whenever its oral tentacles touched the other individual's body during a lunge. Both animals were writhing the front half of their body and repeatedly bristling and lowering all their cerata. The biting failed to wound the opponent as far as we could see, and no appendages were lost. Neither specimen was crawling during the encounter and no active pursuit took place.

These observations have been reported because they open new doors into the behavior and natural history of *Pteraeolidia ianthina*. For instance it has recently been hypothesized that because this aeolid has a symbiosis with zooxanthellae it "never or seldom needs to feed" (RUDMAN, 1986, 1987). I would suggest that feeding is not rare at all in *P. ianthina*; it is just rarely observed.

I am most grateful to Messrs. Robert McGill and Derek Firman for sharing with me their observations of adult *Pteraeolidia ianthina* feeding on hydroids and to Mr. McGill for allowing me to reproduce his photograph. Mrs. Jan Watson identified the hydroid from this photograph. Dr.

Figure 1

Pteraeolidia ianthina consuming the athecate hydroid *Ralpharia magnifica*. 1 December 1985. Photograph: R. McGill.

Terrence Gosliner first noticed the aggressive individuals of *P. ianthina* and attracted my attention to watch them (he subsequently observed another similar encounter). I wish to thank him, Mr. David Brunckhorst, Mr. McGill, and an anonymous referee for comments on an earlier version of this manuscript.

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The Occurrence of Living Mollusks on *Diopatra* Tube-Caps

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Introduction

Tube-caps of the onuphid polychaete *Diopatra* were shown by BELL & COEN (1982) to serve as a substrate for a variety of meiofauna, and other researchers have discussed larger organisms found in association with tube-caps (*e.g.,* MANGUM *et al.,* 1968; WOODIN, 1978; GALLAGHER *et al.,* 1983; BAN & NELSON, 1987; LUCKENBACH, 1987). In the present note we report specifically on the ubiquitous presence of epibiont mollusks on tube-caps at three widely separated collecting sites.

Materials and Methods

Thirty-six tube-caps (12 from each site) were collected by hand at low tide from three moderately protected sand flats: *Diopatra ornata* (Moore, 1911) from Venado Beach, Pacific coast of Panama (February 1986); and *Diopatra cuprea* (Bosc, 1802) from Tom's Cove, Assateague National Seashore, Virginia, U.S.A. (June 1987) and from Wheeler's Beach, Woods Hole, Massachusetts, U.S.A. (July 1987). The Panama and Assateague specimens were air-dried and individually packaged until examined; the Woods Hole specimens were examined within a day of collection. Each tube-cap was examined under a dissecting microscope for epibiont mollusks. Shells of dead mollusks that had been attached by the worm to its tube-cap were identified but were not included in the data. Mollusks that had been alive at the time of collection were recognized in the following ways: gastropods were relatively unworn and had shining apertures and undamaged margins, or (as in the case of *Crepidula* species) were still attached to shell fragments or to the tube itself; bivalves had both valves still connected and closed; and the chitons were still attached to fragments embedded in the tube. Once the epibiont mollusks had been isolated they were identified to the lowest possible taxon. (Panama mollusks were identified by the senior author, using KEEN, 1971; the Assateague and Woods Hole species were familiar to all the authors.)

Table 1

Molluscan species found on 12 *Diopatra* tube-caps at each of three sites (numbers of individuals in parentheses).

Panama
Anachis sp. (4)
Crepidula sp. *cf. excavata* (Broderip, 1834) (23)
Crucibulum sp. (2)
Nassarius (*Arcularia*) *complanatus* (Powys, 1835) (1)
Notoacmaea sp. *cf. subrotundata* (Carpenter, 1865) (1)
Terebra sp. (2)
Theodoxus (*Vittoclithon*) *luteofasciatus* Miller, 1879 (7)
Chione sp. (3)
Modiolus sp. (1)
Nuculana sp. (1)
Sphenia fragilis (H. & A. Adams, 1854) (3)
Unidentified chiton species (3)
Assateague
Crepidula convexa Say, 1822 (1)
Crepidula fornicata L., 1758 (1)
Mercenaria mercenaria (L., 1758) (11)
Unidentified bivalve species (1)
Woods Hole
Crepidula convexa (2)
Crepidula fornicata (2)
Littorina littorea (L., 1758) (3)
Nassarius trivittatus (Say, 1822) (3)
Seila adamsi (Lea, 1845) (1)
Anadara transversa (Say, 1822) (2)
Mya arenaria L., 1758 (2)

Results and Discussion

Twenty-one species and 80 individuals, none greater than 10 mm in length, were found on the examined *Diopatra* tube-caps (Table 1). The Panamanian tube-caps each had two or more epibiont mollusks (up to nine on one individual), whereas those from Assateague and Woods Hole often had none or only one (Table 2). Gastropods, bivalves,

Table 2

Distribution of mollusks on 12 *Diopatra* tube-caps from each site.

Site	Number of individual mollusks per tube-cap									
	0	1	2	3	4	5	6	7	8	9
Panama			3	3	2		2	1		1
Assateague	6	2	3				1			
Woods Hole	3	6	1	1	1					

and chitons were present, with gastropods being the most abundant, comprising 57% of the species and 66% of the individuals.

These results show that the crevices formed by the shells, shell fragments, and other debris incorporated into *Diopatra* tube-caps by their builders offer a previously unrecognized substrate for mollusks. It is particularly interesting that almost half of the species represented—all the *Crepidula* spp., *Theodoxus luteofasciatus, Anachis* sp., *Sphenia fragilis,* the chiton, *Crucibulum* sp., *Notoacmaea cf. subrotundata,* and *Seila adamsi*—are hard-bottom organisms. In the broad expanse of sand flats, *Diopatra* tube-caps may therefore represent a valuable resource, especially for those smaller species that could attain sexual maturity while living on this space-limited substrate. How effective tube-caps are as possible refuges from predation (small mollusks on sand flats can be subject to heavy predation pressure, *e.g.,* DUDLEY, 1980) or as long-term settlement sites for young individuals of species such as *Mercenaria mercenaria* that can attain large adult sizes, are questions to be resolved by an experimental approach. In view of the apparently widespread use of tube-caps by mollusks that this study documents such questions are worthy of investigation.

Acknowledgments

We thank Erik Rensberger, Kendra Richardson, Barbara Schuel, Hilary Specht, and Amber Ulbrich for helping us gather data; Dr. and Mrs. Paul Wheeler for the use of their beach to collect specimens; and the staff at the Woods Hole Marine Biological Laboratory for the use of the library.

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Dietary-Induced Hyperlipidemia in *Biomphalaria glabrata* (Gastropoda)

by

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Introduction

The planorbid snail *Biomphalaria glabrata* (Say, 1818) is an intermediate host of the medically important trematode *Schistosoma mansoni,* and has been used for numerous physiological and biochemical studies. Relatively little information is available on lipids in this snail, although a recent study examined lipids in fed and starved *B. glabrata* (DUNCAN *et al.,* 1987).

Information on dietary-induced hyperlipidemia in this snail is not available. Unpublished studies in our laboratory show that *Biomphalaria glabrata* fed a high lipid diet, *i.e.,* hen's egg yolk, ingest and utilize the material, grow, and lay eggs. The purpose of this study is to determine if snails fed hen's egg yolk elevate their lipids compared to snails fed leaf lettuce. *Biomphalaria glabrata* may serve as a useful invertebrate model to study dietary-induced hyperlipidemia in humans.

Materials and Methods

Snails, 10 ± 2 mm in shell diameter, were removed from stock cultures, placed in artificial spring water (DUNCAN *et al.,* 1987) and fed boiled hen's egg yolk (experimentals) or leaf lettuce (controls) *ad libitum.* Food and water were changed every other day, and some snails on experimental and control diets were removed for examination 1 and 2 weeks after the cultures were initiated.

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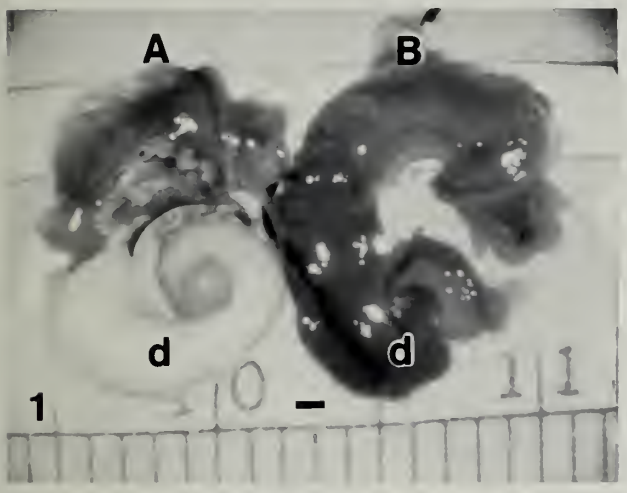

Figure 1

A photograph of live *Biomphalaria glabrata* snails fed hen's egg yolk (A) or leaf lettuce (B) for 2 weeks. Shells were removed to expose the body. The digestive gland-gonad complex (d) is white in the yolk-fed snail and green-brown in the lettuce-fed snail. Scale bar = 1 mm.

Two groups of 10 snails each, maintained for 1 or 2 weeks on either a yolk diet or lettuce diet, were analyzed gravimetrically. The whole snail (with shell) was weighed and then extracted with 3 mL of chloroform/methanol (2:1). Non-lipid contaminants were removed with the Folch wash (0.88% KCl), and the lipid extract of each snail was dried under nitrogen and weighed to determine the percentage of total lipid.

For most chromatographic analyses, one or two snails were treated as mentioned for the total lipid gravimetric analysis. For TLC studies the snail lipid extract was spotted on individual lanes in the preadsorbant area of a 20 × 20-cm precoated silica gel plate (Whatman LK6DF, Whatman Inc., Clifton, New Jersey). On the same plate was spotted 3 μL of the neutral lipid standard 18-4A (Nu-Chek Prep, Elysian, Minn.), consisting of 0.2 μg/μL each of cholesterol, oleic acid, triolein, methyl oleate, and cholesteryl oleate. Plates were developed 12 cm past the origin in a saturated glass rectangular tank with petroleum ether-diethyl ether-acetic acid (80:20:1). The lipids were detected by dipping the plates in 5% phosphomolybdic acid in ethanol and heating them in an oven at 100–120°C for approximately 5–10 min. The lipids appeared as blue-gray spots against a yellow background. Relative amounts of lipids were estimated by visual comparison of spot intensities between sample and standard chromatograms.

For capillary gas chromatography the lipid extracts of six snails fed lettuce and six snails fed yolk for 1 week were separated on preparative silica gel plates (Whatman PK1F, 1-mm layer thickness, Whatman Inc., Clifton, New Jersey) developed for 12 cm in petroleum ether-diethyl ether-acetic acid (80:20:1). Bands were scraped from the plate, packed in a microcolumn, and the sterols eluted with chloroform (Fried & Sherma, 1986). The sample was dried and reconstituted to 10 μg/μL with chloroform-methanol (2:1).

The sterols were analyzed by injecting 1 μL of sterol sample and standards (1 μg/μL solutions) into a Hewlett-Packard H-P 5890 gas chromatograph equipped with an H-P 3992A integrator/recorder, flame ionization detector, and a 15-m fused silica column (SPB-1) operated with a 1/30 split injection ratio and 270°C isothermal temperature for 25 min. Retention times of peaks in the samples were compared to those of standards for identification.

Table 1

TLC analysis of neutral lipids of whole snails fed lettuce (L) or yolk (Y) for 1 or 2 weeks.

Lipid classes	R_f values*	Week 1		Week 2	
		L	Y	L	Y
Free sterols	0.18	2	2	2	2
Free fatty acids	0.30	0	1	0	1
Triacylglycerols	0.70	1	3	1	3
Sterol esters	0.94	1	2	1	2

Key: none = 0; trace = 1; moderate = 2; heavy = 3.

* Determined for 20 × 20-cm silica gel Whatman LK6DF plates developed for 12 cm from the origin in 100 mL of petroleum ether-diethyl ether-acetic acid (80:20:1) at 22–24°C.

For lipid histochemistry, four yolk-fed and four lettuce-fed snails, maintained on the diets for 2 weeks, were sectioned at 10 μm on a cryostat, and stained with Oil Red O (Lillie, 1944).

Results and Discussion

The yolk-fed snails developed a white digestive gland-gonad complex while that of lettuce-fed snails remained green-brown (Figure 1). Regardless of the diet more than 90% of the snails were alive 2 weeks after the experiments were initiated.

Total lipid of whole yolk-fed *Biomphalaria glabrata* was compared with that of lettuce-fed snails. The yolk-fed snails (n = 10) had an average percent lipid of 2.53 ± 0.14, whereas the lettuce-fed snails (n = 10) had an average percent lipid of 1.68 ± 0.14. The increase in lipid occurred mainly in the digestive gland-gonad complex.

TLC showed a marked increase in the triacylglycerol fraction of yolk-fed snails at 1 and 2 weeks and a less marked increase in the free fatty acid and sterol ester fractions; an increase in the free sterol fraction was not apparent in yolk-fed snails (Table 1). When the sterol fraction was analyzed by GLC it was found, for both lettuce-fed and yolk-fed snails, that cholesterol was the major fraction with other sterols being present in smaller amounts. Sterols in both snails were campesterol, stigmasterol, and β-sitosterol. The yolk-fed snails in addition had desmosterol, coprostanol, and ketocholesterol.

The digestive gland-gonad complex of yolk-fed snails contained abundant lipid droplets stained with Oil Red O ranging in size from 20 to 40 μm. The same complex of lettuce-fed snails contained relatively few lipid droplets ranging in size from 5 to 10 μm.

Acknowledgment

We thank the Dow Chemical Co. Foundation, Midland, Michigan for supporting the undergraduate research of S.S.

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Range Correction for *Agaronia propatula* (Conrad, 1849)

by
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Lopez *et al.* (1988) report *Agaronia propatula* (Conrad, 1849) from Bahia de los Angeles, Baja California. The shells were actually collected by me near the type locality of *Epitonium textimatum* DuShane, 1977, at Playa de los Angeles, Tenacatita Bay, Jalisco, Mexico (see map in DuShane, 1977).

The correct range for the species should be from Jalisco, Mexico, to Panama.

Literature Cited

DuShane, H. 1977. *Epitonium textimatum,* a new gastropod from the west coast of Mexico. Nautilus 91:89–91.

Lopez, A., M. Montoya & J. Lopez. 1988. A review of the genus *Agaronia* (Olividae) in the Panamic Province and the description of two new species from Nicaragua. Veliger 30: 295–304.

Worldwide Chiton Collection Available for Loan

A collection of chiton specimens, which previously formed a part of the collection of Dr. Ian McTaggart-Cowan, has been catalogued at the Royal British Columbia Museum. Many worldwide localities are represented, although most specimens come from British Columbia and the western coast of North America. Specimens are available for loan to scientists interested in studying the systematics, distribution, or taxonomy of this molluscan group. Most specimens are fluid preserved, although some are dry dorsal plates only. The collection contains 19 paratypes from 4 locations (Peden & Green, 1981, *Syesis* 14:155–162).

Requests for further information regarding this collection should be directed to:

Grant Hughes, Chief, Biological Collections, or
Philip Lambert, Head, Invertebrates
Royal British Columbia Museum
675 Belleville Street
Victoria, British Columbia
Canada V8V 1X4

International Commission on Zoological Nomenclature

The following Opinion of potential interest to our readers has been published by the ICZN in the *Bulletin of Zoological Nomenclature,* volume 45, part 3, on 23 September 1988:

Opinion No. 1502. *Conus fergusoni* G. B. Sowerby III, 1873 (Mollusca, Gastropoda): specific name conserved.

The following application has been published on 16 December 1988 in volume 45, part 3 of the *Bulletin of Zoological Nomenclature.* Comment or advice on this application is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, ICZN, British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.

Case 2643. *Iphinoe* Bate, 1856 (Crustacea, Cumacea): proposed conservation.

Conservation of the generic name *Iphinoe* Bate, 1856, of cumacean crustaceans involves the suppression of the gastropod name *Iphinoe* H. & A. Adams, 1854.

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The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

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a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

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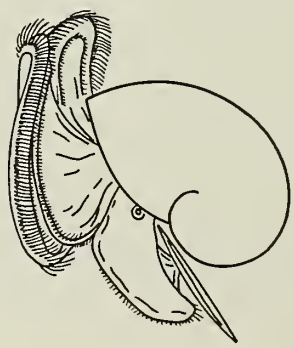

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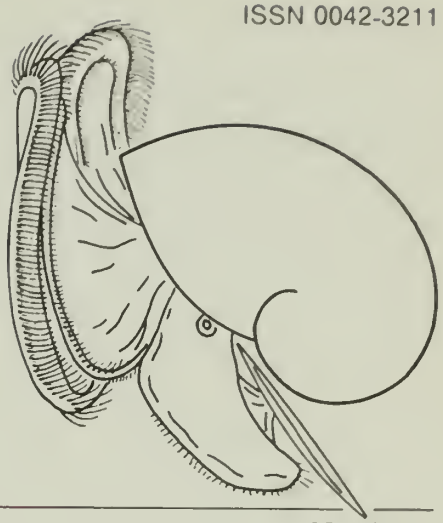

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Shell Morphometrics and Systematics: A Revision of the Slender, Shallow-Water *Cadulus* of the Northeastern Pacific (Scaphopoda: Gadilida)

by

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Abstract. The shell morphologies of 15 populations of eastern Pacific *Cadulus* species with slender shells were quantitatively examined and compared. Indices of shell shape were constructed relating total shell length to length from the dorsal aperture to the maximum width (LI), and maximum shell diameter to apertural diameter (WI). Using these indices, and Ws, the rate of whorl expansion, *Cadulus fusiformis, C. hepburni,* and *C. nitentior* were determined to be junior synonyms of *C. aberrans.* The indices were shown to be replicable and useful in distinguishing between shells of very similar shape.

Cadulus aberrans is redescribed using the above indices, including measures of the variability of shell shape, and ecological characteristics.

The shell shape of these slender scaphopods likely arose to facilitate escape from predators. Some aspects of scaphopod shell shapes, particularly dorsal apertural lobation, and secondary shell tubes are likely too variable to be useful as generic-group characters.

INTRODUCTION

Four nominal species of slender scaphopod mollusks of the genus *Cadulus* are synonymized as a result of the construction and comparison of indices based on shell morphometry. The indices were constructed from measurements taken of two large samples collected from different northern populations and from smaller samples of several southern populations. One purpose of this paper is to assess variability of several measures of shell morphology. Secondly, I use these indices in conjunction with the examination of type material to determine synonymies within this group of nominal species, and to redescribe the species occurring north of central California. Where possible, and when relevant, I present data on other aspects of the morphology of these species.

I have defined the slender *Cadulus* (Figure 1) as those scaphopods with a polished shell, a total length of less than 15 mm, and an anterior or oral (anatomically ventral) aperture that is from 0.8 to 1.0 times the maximal shell diameter. If the maximal width of the shell is located posterior (anatomically dorsal) to the ventral aperture, it is in the anterior third of the shell. Although curved, with the concave portion of the curve on the dorsal (anatomically anterior) side of the animal, the curve is not pronounced. In the northeastern Pacific the nominal taxa of *Cadulus* with these characters are *C. aberrans, C. hepburni, C. fusiformis, C. nitentior, C. perpusillus* (Pilsbry & Sharp, 1897–1898; Grant & Gale, 1931; Keen, 1971; Abbott, 1974; Emerson, 1971; Baxter, 1987). The more typical *Cadulus* forms, represented in this area by several species, particularly *C. tolmiei* and *C. californicus,* differ from the slender species in that they have a pronounced narrowing at the ventral aperture, and the widest part of the shell, often twice or more the width of the aperture, is located in the middle third of the shell.

All these species were described prior to 1910 utilizing only the most basic shell characteristics; the original descriptions were generally qualitative and uniformly brief, and little or no effort was devoted to determination or mention of variability (Whiteaves, 1887; Dall, 1897; Pilsbry & Sharp, 1898; Arnold, 1903). Additionally, relatively few consistent shell measurements were made; thus, construction of various discriminatory indices has been difficult. As the various malacologists and major collections of the period were scattered, and comparison between the collections apparently uncommon, and as spec-

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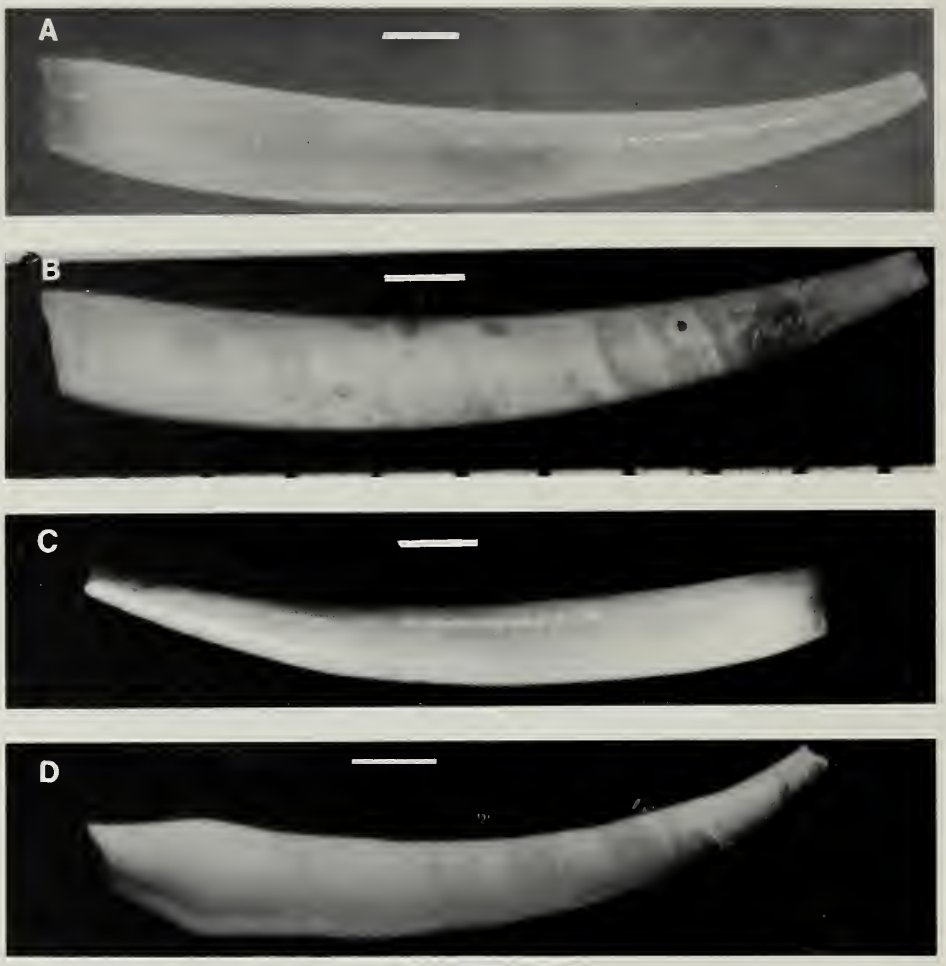

Figure 1

Cadulus types and specimens. Scale bar = 1 mm. A. *C. aberrans* Whiteaves, 1887, largest syntype. National Museums of Canada No. 555. B. *C. hepburni* Dall, 1897, figured type. USNM No. 107612. C. *C. fusiformis* Pilsbry & Sharp, 1898, lectotype. USNM No. 133809. D. *C. perpusillus* (Sowerby, 1832). Typical specimen from population LACM8, 31.12°N.

imens were collected relatively infrequently, several descriptions of small slender scaphopods assignable to *Cadulus* were published (Whiteaves, 1887; Dall, 1897; Pilsbry & Sharp, 1897–1898; Arnold, 1903).

These small scaphopods, often common in the subtidal soft-sediment habitats of the Pacific Coast of North America (Shimek, 1988), are seldom found at depths less than 20 m, but are frequently collected from deeper areas, and some species appear to be widespread (Abbott, 1974; Baxter, 1987).

During a study of the ecological interactions of a multispecies scaphopod assemblage found in the Barkley Sound region of Vancouver Island, British Columbia (Shimek, in prep.), I collected large numbers of scaphopods, including several hundred small *Cadulus* assignable to at least three species.

With this large sample from one region as a basis, I have made a detailed examination of shell morphology utilizing several replicable measurements. These measurements allow the construction of reliable indices that can be used not only to describe and discriminate among the species in question, but also to quantitatively examine shell morphological variation within and between populations.

Finally, the relationship of some supra-specific characters within the class Scaphopoda are briefly discussed. Some of the presently accepted taxonomic characters within the class are spurious and have been used because of insufficient knowledge of the living animals.

SYSTEMATIC ACCOUNT

Cadulus aberrans Whiteaves, 1887:124, fig. 2. Type locality: Quatsino Sound, Vancouver Island, British Columbia, in 30–50 fm (55–92 m).

Cadulus hepburni Dall, 1897:12, pl. 1, fig. 13. Type locality:

Near Victoria, Vancouver Island, British Columbia, in 60 fm (110 m).

Cadulus fusiformis PILSBRY & SHARP, 1898:193, pl. 35, fig. 14. Type locality: San Pedro, California, at 150 foot (46 m) depth. Also known, as a fossil, from San Diego, California.

Cadulus nitentior ARNOLD, 1903:187, pl. 8, fig. 13. Type locality: Pleistocene, Deadman Island, San Pedro bluffs, California.

REDESCRIPTION OF *Cadulus aberrans*

External Anatomy

Shell: Shell slender, length to maximum width ratio = 0.13 ± 0.02, slightly curved, ln(Ws) = 6.076 ± 1.231 (Ws = whorl expansion rate = 1344 ± 4607); highly polished, lustrous, translucent white; minute growth lines present (visible with magnification only); ventral (=oral or anterior) aperture oblique, round; dorsal (=anal, or posterior) aperture round, not lobed. No dorsal secondary apertural tube (such as found in *Dentalium*). Juvenile specimens, to about 10 mm in total length, without constriction of ventral aperture. Adult size determinate, total length to about 13 mm; adult specimens with slightly constricted aperture (WI = Width Index = ln(ApW + 1)/ln(Wm + 1) = 0.852 ± 0.063). Maximal width near anterior end (LI = Length Index = ln(LWm + 1)/ln(LTot) = 0.513 ± 0.055). Shell lip thin and sharp.

Soft part morphology: The mantle is generally dull white, except for a golden ring at area of outer mantle fold. When extended out of the ventral aperture, the mantle has a triradiate fold. The foot extends through the center of this triradiate area. The mantle may protrude about 1 mm beyond the dorsal aperture in an adult (shell length > 10 mm). There are no consistent sexual differences in the shape of the "pavilion," or tube formed from the dorsal mantle edge, in living animals.

The foot is extendable to the length of the shell, caduliform, with a terminal disk, and papillate laterally; sometimes one or two small papillae are visible on the distal face of the terminal disk.

Captacula are numerous, over 100 in adults, and extendable to 2–3 mm; the terminal bulb is densely ciliated, and stalk cilia are limited to tufts arranged linearly (SHIMEK, 1988).

Visible internal morphology: The radula is visible through the shell, brownish, and highly mineralized, with most highly mineralized areas being black; the radular formula is 1·1·1·1·1; the marginal teeth are large and platelike; the lateral teeth are hooked, with two cusps, and the central tooth is small. All teeth are mineralized with iron and calcium salts.

The cerebral ganglia are visible through the shell ventral (=anterior) to radular mass, and are pinkish.

The digestive gland is dark brown to black, prominent, and visible through the shell.

The gonads are visible through the adult shells. The gonads are brilliant white in males and brown in females; ova are brown.

Ecological Characteristics—British Columbia Specimens

Specimens are found in clean, well-sorted sand; the depth distribution is 20–100 m, and the population density 6–10/m^2. The animal is a predator on small (maximal dimension generally <0.300 mm) live foraminiferans; it prefers *Rosalina* cf. *columbiana* (Cushman, 1925), *Cribrononion lene* (Cushman & McCulloch, 1940), rejects (eats fewer than would be expected) *Florilus basispinatus* (Cushman & Moyer, 1930), and eats *Elphidiella hannai* (Cushman & Grant, 1927) as encountered. The most abundant minor prey species are *Buliminella elegantissima* (d'Orbigny, 1839) and *B. exilis* (H. B. Brady, 1884); other foraminiferan species are occasionally taken. Prey are maintained in a buccal pouch (=proboscis) prior to maceration, and individuals may have up to 125 foraminiferans in the pouch.

Geographical Range

Southern California through Prince William Sound, Alaska.

Lectotypes

I here designate the following specimens as lectotypes of *Cadulus aberrans* Whiteaves, 1887:

Cadulus hepburni Dall, 1897, USNM No. 107612;
Cadulus fusiformis Pilsbry & Sharp, 1898, USNM No. 133809;
Cadulus nitentior Arnold, 1903, USNM No. 23729.

MATERIALS AND METHODS

Type or Reference Specimens Examined

The following *Cadulus* type or reference specimens were examined: *C. aberrans* Whiteaves, 1887, National Museums of Canada catalogue number 555, 5 specimens, all syntypes; *C. hepburni* Dall, 1897, United States National Museum of Natural History (USNM) catalogue number 107612, 1 specimen, a paratype, the figured type; *C. fusiformis* Pilsbry & Sharp, 1898, USNM number 133809, a lectotype, designated by Pilsbry & Sharp, 1898; *C. nitentior* Arnold, 1903, *ex* Carpenter MS, USNM number 23729 (not type); *C. perpusillus* Sowerby, 1832, photo of lectotype, USNM number 96570, designated by EMERSON (1971:fig. 1); *C. californicus* Pilsbry & Sharp, 1898, USNM number 107698, a lectotype; *C. tolmiei* Dall, 1897, USNM number 107613, figured paratype.

The types, reference specimens, or photographs listed above were examined and measured (Figure 1, Table 1). I was not able to physically examine the types of *Siphonodentalium quadrifissatum* (Pilsbry & Sharp, 1898) and *Ca-*

Table 1

Measurements taken of *Cadulus* type and reference specimens examined. See the text for the appropriate transformation.

	Transformed measurements				Derived indices		
Species of *Cadulus*	lnLTot	lnApW1	lnWm1	lnLWm1	LI	WI	Ws
aberrans							
1	2.41	0.77	0.86	1.10	0.46	0.90	395
2	2.40	0.82	0.92	0.82	0.34	0.89	107
3	2.49	0.75	0.85	0.85	0.34	0.88	323
4	2.54	0.88	0.97	1.15	0.45	0.91	135
5	2.43	0.78	0.85	0.94	0.39	0.93	477
californicus	2.69	1.13	1.40	1.58	0.59	0.81	343
fusiformis	2.26	0.63	0.78	0.65	0.29	0.80	2601
hepburni	2.33	0.80	0.88	0.80	0.34	0.91	1396
nitentior	2.16	0.72	0.81	1.23	0.57	0.88	100
perpusillus	1.96	0.49	0.66	0.54	0.27	0.85	255
tolmiei	2.43	1.02	1.19	1.55	0.64	0.86	261

dulus perpusillus; however, measurements of the latter were made from published illustrations of the lectotype designated by EMERSON (1971:fig. 1). Although I did not examine the figured type of *C. nitentior,* I examined Carpenter's specimen from the U.S. National Museum of Natural History that was used in Arnold's determination of this species (ARNOLD, 1903). The figured individual was a different, more eroded, individual than that used in the description.

Experimental Material Examined

In addition to the types, I examined specimens of slender *Cadulus* collected at 15 localities along the west coast of North America from 24°N to about 50°N and from a considerable depth range. Collection data from the 15 localities are as follows: population LACM1, from 23.52°N, 109.00°W, collection depth 9 m, 27 individuals, none were juveniles; population LACM2, from 24.18°N, 111.35°W, collection depth 69–87 m, 10 individuals, no juveniles; population LACM3, from 24.23°N, 110.03°W, collection depth 250–400 m, 5 individuals, 1 juvenile; population LACM4, from 27.21°N, 114.53°W, collection depth 107–129 m, 11 individuals; population LACM5, from 27.69°N, 115.09°W, collection depth, 89 m, 13 individuals, 4 juveniles; population LACM6, from 27.95°N, 115.13°W, collection depth 31–36 m, 40 individuals, 1 juvenile; population LACM7, from 29°N, 113°W, collection depth 18–36 m, 6 individuals, 1 juvenile; population LACM8, from 31.12°N, 114.82°W, collection depth 7–11 m, 133 individuals, no juveniles; population LACM9, from 33°N, 118°W, collection depth 25 m, 6 individuals, no juveniles; population LACM10, from 33.47°N, 118.48°W, collection depth 82–91 m, 2 individuals, no juveniles; population LACM11, from 33.58°N, 118.42°W, collection depth 14 m, 6 individuals, no juveniles; population LACM12, from 36.63°N, 121.90°W, collection depth 36 m, 101 individuals, 20 juveniles; population LACM13, from 48.41°N, 126.10°W, collection depth 274 m, 9 individuals, no juveniles; population DS, from 48.43°N, 125.50°W, collection depth 100–150 m, 92 individuals, 31 juveniles; population T, from 48.83°N, 125.18°W, collection depth 18–91 m, 334 individuals, 101 juveniles. Thus a total of 794 individuals were examined, of which 159 or 20.03% exhibited the juvenile shell morphology.

For outgroup comparisons I examined *Dentalium rectius* Carpenter, 1864, *Pulsellum salishorum* Marshall, 1981, and *C. tolmiei* Dall, 1897, a more typical *Cadulus* species. All were collected from Barkley Sound, on the southwest side of Vancouver Island. Thirty specimens of *C. tolmiei* were collected from a depth of 150–350 m at Sarita Bay, 48.89°N, 125.05°W. *Dentalium rectius* and *P. salishorum* were collected from three localities: Mayne Bay, 48.98°N, 125.33°W, collection depth 35–40 m; Imperial Eagle Channel, 48.88°N, 125.19°W, collection depth 75–80 m; and Trevor Channel, 48.83°N, 125.18°W, collection depth 30–110 m. Collections from the above sites were pooled, yielding for comparison 483 individuals of *D. rectius* and 283 individuals of *P. salishorum.*

Measurements

For all the specimens, unless otherwise noted, I measured total length (LTot), length from the most anterior position of the ventral aperture of the shell to the widest portion of the shell (LWm), length from the ventral aperture to the place of maximum arc (Larc), the interior ventral aperture width (ApW), the maximum width (Wm), and the maximum arc (arc). As the measurement orientation is important for replication, the exact orientation of the measurements is indicated (Figure 2). All measurements, unless otherwise noted, were taken using a stereo dissection microscope with a calibrated ocular micrometer at magnifications of 10 (*Dentalium rectius*) to 40 diameters (*Cadulus* spp. and *Pulsellum* sp.). The lobes around the dorsal aperture were counted. All linear measurements

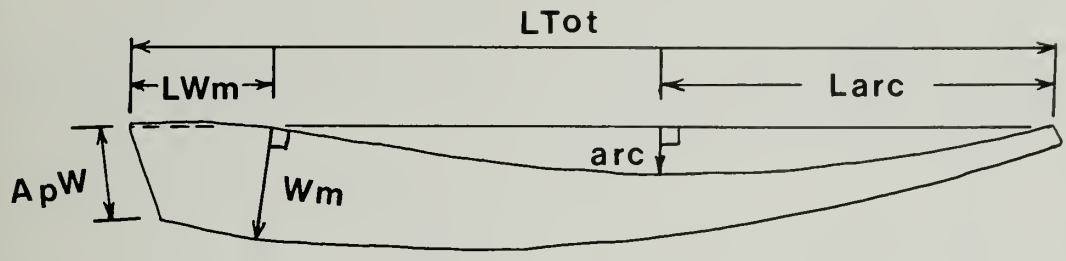

Figure 2

Measurements taken of all specimens; all orientations labeled anatomically; *i.e.*, the foot is ventral. Abbreviations: ApW = interior width of the ventral aperture, measured perpendicular to the anteriormost shell surface; arc = maximum perpendicular distance from a line connecting the anteriormost margin of the dorsal aperture to the anteriormost margin of the ventral aperture to anterior surface of the shell; Larc = distance from the anteriormost margin of the dorsal aperture to the point where the arc was measured; LTot = total length, from anteriormost margin of the dorsal aperture to the anteriormost margin of the ventral aperture; LWm = length to point of maximum width, from the anteriormost margin of the ventral aperture to the anteriormost point of the widest part of the shell; Wm = maximum shell diameter, measured perpendicular to the anteriormost surface of the shell at that point.

were converted to their natural logarithms to minimize problems of size scale for comparison. As index calculations involving LWm, ApW, and Wm might result in terms less than or equal to zero, resulting in the natural logarithms being either negative or undefined, one (1) was added to each of these terms for calculation purposes.

Derivation of Indices

From these measurements, the following indices were defined. LI = ln(LWm + 1)/ln(LTot); WI = ln(ApW + 1)/ln(Wm + 1). The whorl expansion rate (Ws) (Raup, 1966) was also calculated. Scaphopods never complete one entire whorl; however, the index could be derived from the measurements taken of the scaphopod shells.

$$\text{Whorl expansion rate} = Wa^{\frac{\theta}{2\pi}} = \frac{R_i}{R_0} \qquad \text{(Raup, 1966)}$$

Let R_i = LTot, and $R_0 = \sqrt{(\text{LTot} - \text{Larc})^2 + (\text{arc})^2}$.

$$\text{Then } Wa^{\frac{\theta}{2\pi}} = \frac{\text{LTot}}{\sqrt{(\text{LTot} - \text{Larc})^2 + (\text{arc})^2}}$$

$$\text{And } Ws = Wa^{\left(\frac{1}{\frac{\theta}{2\pi}}\right)} = Wa^{\frac{2\pi}{\theta}}$$

$$\text{And } \frac{\theta}{2\pi} = \text{atan}\,\frac{\text{arc}}{\text{LTot} - \text{Larc}}$$

Thus Ws

$$= \frac{\text{LTot}}{(\sqrt{(\text{LTot} - \text{Larc})^2 + (\text{arc})^2}} \left(\frac{1}{\text{atan}\left(\frac{\text{arc}}{\text{LTot} - \text{Larc}}\right)}\right)$$

For comparisons between populations, I used the natural logarithm of the population median values of Ws. The medians were less sensitive to extreme values and, thus, were better indicators of central tendency. The use of the logarithms eliminated some of the problems caused by comparisons over several orders of magnitude.

For morphometric comparisons, except for *Cadulus tolmiei*, I used shells with clearly adult morphology. Where necessary, I eliminated from the comparison specimens missing one or more of the measurements. Various measurements might be unreliable owing to breakage or changes in curvature resulting from healed fractures. I used the largest possible data set for each test and/or comparison. Consequently, differing comparisons of the same population sometimes varied slightly in the total number of individuals. No more than 10 specimens were ever removed from any comparison by this arbitrary method.

Buccal content analyses were done using methods described in Bilyard (1974) and Shimek (1988).

RESULTS

Determination of Mature Individuals

A number of individuals from some populations did not have the typical *Cadulus aberrans* shape (with the widest part of the shell one-third or less the distance from the ventral to the dorsal aperture); instead the widest part of the shell was at the ventral aperture. Although these animals tended to be smaller in total length than those with the normal morphology, in the northern populations particularly, many were relatively large and apparently sexually mature (Figure 3).

I found no shells intermediate between these "non-bulging" and the more typical "bulging" *Cadulus aberrans* shapes (Figure 3). Thus it was possible that these two morphologies represented two distinctly different species with similar, but subtly different shell shapes.

I did buccal content analyses of specimens of both shapes collected from area T, 48.83°N, from June to December 1984. The variety and proportion of dietary items from both sets of specimens were similar, and the dietary over-

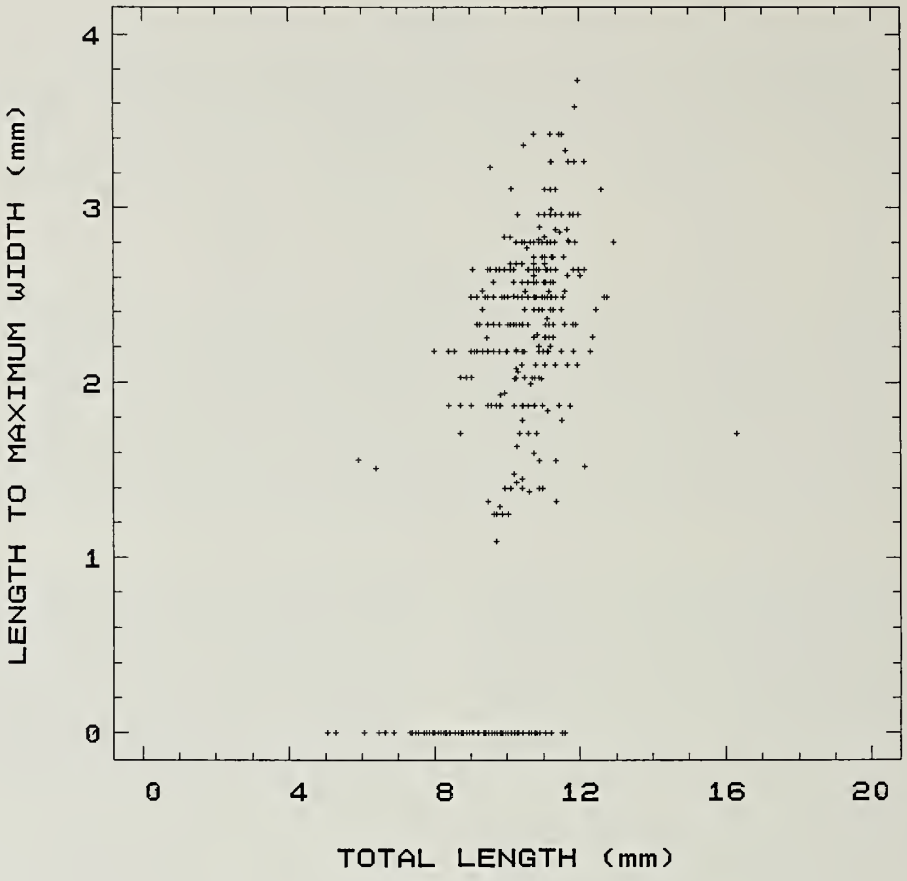

Figure 3

Adult and juvenile *Cadulus aberrans* from pooled populations DS and T. Ordinate = length from the ventral aperture to the point of maximum width; Abscissa = total shell length. Upper cluster of points (n = 294) is animals with the typical adult morphology (*i.e.*, a constricted ventral aperture). The lower line (n = 132) represents those animals without a ventral apertural constriction, *i.e.*, juveniles.

lap, as measured by the least common percentage index (D) (SCHOENER, 1968), was high (Table 2). Nevertheless, the mean dietary foraminiferan size from the animals with the "bulging" morphology was significantly larger (Table 3). There were, however, no statistically significant differences in either the sizes or distributions of the other buccal contents (Table 3). *Cadulus aberrans* is a specialist predator on foraminiferans (SHIMEK, 1988). Consequently, the predominance of foraminiferans meant that the average item in the pooled buccal contents from the bulging animals was significantly larger than that from the contents of the "non-bulging" animals (Table 3).

No single foraminiferan species, however, accounted for this difference in prey size, and, in fact, none of the major prey species was found to be significantly larger in the buccal contents of the "bulging" morphology (Table 4). Rather, the aggregate total distributions are statistically and distinctly different, owing to the larger sample size (Tables 3, 4).

Anatomical examination indicated no distinct difference between those animals with the "bulging" and "non-bulging" morphologies except in the degree of sexual maturity. Some of these "non-bulging" animals appeared to be sexually mature, judging by the visual estimation of the gonadal development. Although I did not note these animals particularly at the time of collection, I estimated them to account for no more than 10% of the "non-bulging" animals. The remainder of the "non-bulging" animals lacked gonads visible through the shell. Although in a few cases the brown pigmentation characteristic of mature females was present in a thin tissue strand lateral to the pedal retractor muscles, gender was indeterminate for most of the "non-bulging" forms; the gonads were simply too small for adequate visual determination through the shell. The adult normal sex ratio is 1:1, but only 28 of the 101 "non-bulging" individuals from area T were clearly female; thus, some individuals were too immature to be sexually differentiated. Consequently, because of the close dietary correspondence, I concluded that these "non-bulging" animals were juveniles or recently sexually mature individuals rather than a different species of similar shape. Thus the data from these individuals could be treated with the remainder

Table 2

Buccal contents of *Cadulus aberrans* collected from area T, 48.83°N. The two morphologies considered here are the "bulging" and "non-bulging" morphologies indicated in the text.

	Morphology			
	Bulging (LI > 0)		Non-Bulging (LI = 0)	
Item	*n*	Proportion	*n*	Proportion
Foraminiferans:	507	0.746	137	0.753
Cribrononion lene	178	0.262	48	0.264
Florilus basispinatus	126	0.185	22	0.121
Elphidiella hannai	53	0.078	15	0.082
Buliminella exilis	49	0.072	17	0.093
Rosalina cf. *columbiana*	32	0.047	11	0.060
Others (11 spp.)	62	0.132	24	0.175
Unidentified foraminiferans	6	0.009	5	0.027
Foraminiferan tests:	55	0.081	24	0.132
Rosalina cf. *columbiana*	21	0.031	10	0.055
Florilus basispinatus	10	0.015	2	0.011
Buliminella elegantissima	8	0.012	2	0.011
Cribrononion lene	6	0.009	7	0.038
Others (6 spp.)	10	0.013	3	0.016
Foraminiferan fragments	101	0.149	13	0.071
Diatom tests	2	0.003	2	0.011
Mineral grains	14	0.021	6	0.033
Sediment bolus	1	0.001	0	—
Total	680	1.000	182	1.000

Dietary overlap between adults and juveniles = D = 0.810.

Table 3

A comparison of buccal contents of "bulging" and "non-bulging" (adult and juvenile) *Cadulus aberrans*.

A. Size of Buccal Content Items in Micrometers (Mean ± 1 SD).

	Adult	*n*	Juvenile	*n*
All foraminiferans	153 ± 93	506	126 ± 89	137
Foram. tests	125 ± 68	55	118 ± 55	24
Foram. fragments	87 ± 33	101	100 ± 34	13
All other items*	78 ± 34	17	87 ± 48	8
All others*	139 ± 87	679	121 ± 81	182

* Sediment bolus excluded.

B. Mann-Whitney Pairs Tests Comparing Adult and Juvenile Diets.

	Large sample *z* statistic	Probability of equalling or exceeding *z*	*n*
All foraminiferans	3.850	0.0001	643
Foram. tests	0.171	0.864	79
Foram. fragments	1.286	0.198	114
All other items	0.119	0.906	25
All items	2.847	0.004	861

of the *Cadulus aberrans* data, particularly in the calculation of whorl expansion rate.

Determination of Population Parameters

Cluster analyses of the mean population values for LI and WI and the median population values for Ws gave three distinct groupings containing animals of similar shapes (Figure 4): a northern group and two southern groups, here concluded to be *Cadulus aberrans*, *C. perpusillus*, and *Siphonodentalium quadrifissatum* respectively.

The samples and the determined species follow, along with the disposition of the specimens. Determined to be *Cadulus aberrans* were the individuals in population LACM6, Los Angeles County Natural History Museum (LACM) accession number 71-158, populations LACM9 through 13, LACM accession numbers 122873, 70-115, 65-1, 60-23, and 72-140 respectively, population DS, deposited at the Institute of Ocean Sciences (Canada), Patricia Bay, British Columbia, and population T, deposited in the author's personal collection. *Cadulus perpusillus* was represented by those individuals from the following stations: populations LACM2 through 5, LACM accession numbers 71-16, 69-59, 71-176, and 71-168 respectively, and population LACM8, LACM accession number 68-33. Finally *Siphonodentalium quadrifissatum* was represented by those individuals from populations LACM1 and 7, LACM accession numbers 71-22 and 65-43.

Pair-wise comparisons of the indices (Tables 5–7) clearly indicate the two *Cadulus* populations are significantly different in all three indices. The northern (*C. aberrans*) individuals tapered much more gradually from the widest part of the shell to the aperture (LI was greater) (Tables 5, 6), and the aperture was relatively larger than that of southern (*C. perpusillus*) individuals (WI was greater) (Tables 5, 6). Furthermore, the median whorl expansion rates calculated from the southern populations were generally less than those calculated from the northern ones, indicating a more pronounced shell curvature (Table 6).

The indices showed that *Siphonodentalium quadrifissatum* narrowed more abruptly to the aperture than either *Cadulus* population, while the ratio of apertural width to maximum width was intermediate between the *Cadulus* populations. The rates of whorl expansion were significantly different from the northern *Cadulus* populations, but similar to those of the southern ones (Tables 5–7).

Adult northern *Cadulus* (*C. aberrans*) were longer and had a wider aperture than the southern ones (*C. perpusillus*), but the maximum width was similar. The distance to the maximum width was much greater in northern specimens than in southern ones. Specimens from the population of *Siphonodentalium quadrifissatum* were intermediate between the northern and southern *Cadulus* species

Table 4

Comparison of the buccal content foraminiferans from adult (bulging) and juvenile (non-bulging) *Cadulus aberrans* collected from population T, 48.83°N.

	Morphology							
	Adult			Juvenile			*t*-test on difference of the mean sizes	
	Eaten		Size (μm)	Eaten		Size (μm)		
Foraminiferan species	Number	Percent	(Mean ± 1 SD)	Number	Percent	(Mean ± 1 SD)	Value	*P*
Cribrononion lene	178	35.18	111 ± 38	48	35.04	103 ± 42	1.59	0.113
Florilus basispinatus	126	24.90	233 ± 98	22	16.06	216 ± 100	0.83	0.831
Elphidiella hannai	53	10.67	211 ± 97	15	10.95	165 ± 115	1.55	0.126
Buliminella exilis	49	9.68	60 ± 22	17	12.41	52 ± 16	1.31	0.193
Rosalina cf. *columbiana*	32	6.32	156 ± 49	11	8.03	141 ± 49	0.84	0.403
Others	68	13.24		24	17.52			
All major species	438	86.75	157 ± 93	113	82.48	129 ± 86	2.88	0.004
Total	506	99.99		137	100.01			
Number examined	39			8				

in length, and smaller than either in the other measurements.

Thus the three population groupings differ unambiguously from one another. Furthermore, the within-population variance is relatively small and consistent. My examination was based on samples taken from 23.52°N to 48.83°N. Unfortunately, the samples were not evenly distributed throughout that large geographical range. None-

Table 5

Comparison of the derived indices for the determined species and outgroups. Only the adult morphologies were used in the calculation of the indices except for *Cadulus tolmiei*; see text for explanation. *t*-tests of comparison of the means for each species were calculated from all the specimens of the indicated species as determined by previous analyses. The probability of both means being independently drawn from the same population is given below the unit diagonal, the level of significance is given above it.

		Species					
Index		*C. aber.*	*C. per.*	*S. qua.*	*C. tol.*	*P. sal.*	*D. rec.*
LI	*Cadulus aberrans*						
	Cadulus perpusillus	—	***	***	**	***	***
	Siphonodentalium	<0.001	—	***	***	***	***
	quadrifissatum	<0.001	<0.001	—	n.s.	***	***
	Cadulus tolmiei	<0.001	<0.001	0.686	—	***	***
	Pulsellum salishorum	<0.001	<0.001	<0.001	<0.001	—	n.s.
	Dentalium rectius	<0.001	<0.001	<0.001	<0.001	1	—
WI	*Cadulus aberrans*						
	Cadulus perpusillus	—	***	n.s.	n.s.	***	***
	Siphonodentalium	<0.001	—	***	***	***	***
	quadrifissatum	0.420	<0.001	—	n.s.	***	***
	Cadulus tolmiei	0.105	<0.001	0.685	—	***	***
	Pulsellum salishorum	<0.001	<0.001	<0.001	<0.001	—	***
	Dentalium rectius	<0.001	<0.001	<0.001	<0.001	1	—
lnWs	*Cadulus aberrans*						
	Cadulus perpusillus	—	***	**	n.s.	***	***
	Siphonodentalium	<0.001	—	n.s.	***	***	***
	quadrifissatum	0.041	0.681	—	***	***	***
	Cadulus tolmiei	0.046	<0.001	<0.001	—	***	***
	Pulsellum salishorum	<0.001	<0.001	<0.001	<0.001	—	***
	Dentalium rectius	<0.001	<0.001	<0.001	<0.001	<0.001	—

n.s., not significant at $\alpha = 0.05$; **, significant at $\alpha = 0.05$; ***, significant at $\alpha = 0.001$.

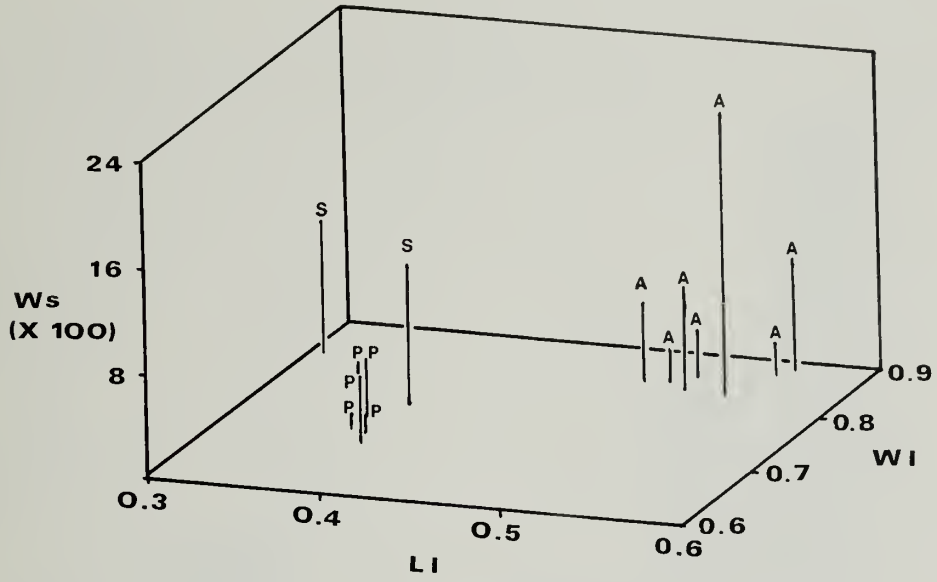

Figure 4

Population clusters generated by the LI, WI, and W indices, calculated for animals with adult morphologies. The LI and WI values used were the mean values for the populations, the Ws value was the population median. A = *Cadulus aberrans*, P = *C. perpusillus*, S = *Siphonodentalium quadrifissatum*. Compare with Tables 5–7.

theless, it is evident that the northern *Cadulus* species has a southern limit at about 28°N, while the southern one extends north to about 31°N. Consequently, there was a zone of overlap. Interestingly, the samples examined showed few signs of having individuals of both species; the estimates of variance for all measurements from populations within the bordering or overlapping areas were no greater than within the more distant ones, and there was no clear geographical pattern in the variation of the mean measurements (Table 6).

DISCUSSION

The relatively constant maximum sizes for the slender *Cadulus* and *Siphonodentalium* species indicate they have a determinate growth pattern. Apparently, once the apertural narrowing occurs, growth in length effectively ceases, although repair of fractures is possible. The large variance in the measurements of *C. tolmiei* seems (Table 7) to argue against a similar growth pattern in this species, but in fact, the pattern is likely the same; a number of juvenile *C.*

Table 6

Derived index values for adults from each of the examined populations.

Population	Latitude	*n*	LI		WI		Ws	
			Median	Mean (±1 SE)	Median	Mean (±1 SE)	Median	Mean (±1 SE)
LACM1	23.52°	27	0.30	0.31 ± 0.01	0.85	0.85 ± 0.01	962	2173 ± 570
LACM2	24.18°	10	0.40	0.39 ± 0.01	0.68	0.69 ± 0.01	501	1961 ± 1328
LACM3	24.23°	4	0.37	0.37 ± 0.02	0.76	0.73 ± 0.06	57	58 ± 13
LACM4	27.21°	11	0.37	0.37 ± 0.02	0.72	0.74 ± 0.02	419	728 ± 210
LACM5	27.69°	9	0.39	0.40 ± 0.03	0.73	0.71 ± 0.03	133	862 ± 454
LACM6	27.95°	39	0.50	0.50 ± 0.01	0.85	0.84 ± 0.01	269	560 ± 136
LACM7	29°	5	0.36	0.34 ± 0.02	0.82	0.81 ± 0.02	57	153 ± 69
LACM8	31.12°	133	0.39	0.38 ± 0.00	0.77	0.77 ± 0.00	1038	2832 ± 449
LACM9	33°	6	0.51	0.49 ± 0.01	0.83	0.83 ± 0.02	593	660 ± 192
LACM10	33.47°	2	0.56	0.56 ± 0.05	0.89	0.89 ± 0.03	853	853 ± 369
LACM11	33.58°	6	0.54	0.54 ± 0.01	0.84	0.83 ± 0.01	2129	5659 ± 3900
LACM12	36.63°	81	0.51	0.51 ± 0.01	0.84	0.84 ± 0.01	736	4186 ± 1074
LACM13	48.41°	9	0.56	0.55 ± 0.02	0.87	0.87 ± 0.01	254	887 ± 541
DS	48.43°	61	0.52	0.51 ± 0.01	0.86	0.83 ± 0.01	451	2533 ± 863
T	48.83°	233	0.52	0.52 ± 0.00	0.86	0.86 ± 0.00	330	540 ± 46

Table 7

Comparative shell morphometrics.

A. Mean (±1 SD) parameters of shell morphology for each of the slender scaphopod species. Calculated on the basis of adult morphology only.

	Cadulus		
	aberrans	*perpusillus*	*Siphonodentalium quadrifissatum*
Measurements (mm)			
LTot	9.97 ± 1.46	7.61 ± 0.98	8.36 ± 0.99
ApW	1.02 ± 0.15	0.87 ± 0.09	0.86 ± 0.07
Wm	1.28 ± 0.19	1.29 ± 0.17	1.09 ± 0.10
LWm	2.27 ± 0.49	1.18 ± 0.22	0.94 ± 0.23
Indices			
LI	0.51 ± 0.06	0.38 ± 0.05	0.31 ± 0.05
WI	0.85 ± 0.06	0.76 ± 0.05	0.84 ± 0.04
ln(Ws)	7.08 ± 1.23	6.67 ± 1.57	6.55 ± 1.51
Latitude range	28°N–49°N>	<24°N–31°N	<23°N–29°N
n examined	430	167	32

B. Comparison of the shell morphology parameters for the other species of scaphopods examined as outgroups.

	Cadulus tolmiei	*Dentalium rectius*	*Pulsellum salishorum*
Measurements (mm)			
LTot	7.97 ± 2.10	27.60 ± 8.79	7.46 ± 1.35
ApW	1.66 ± 0.24	2.03 ± 0.44	1.10 ± 0.11
Wm	1.89 ± 0.30	=ApW	=ApW
LWm	1.33 ± 1.31	0	0
Indices			
LI	0.29 ± 0.28	0	0
WI	0.83 ± 0.22	1	1
ln(Ws)	5.61 ± 1.03*	14.86 ± 7.00	4.63 ± 0.99
Number examined	30	483	283

* Includes juveniles; see text.

tolmiei without the apertural narrowing were measured to increase the sample size for the index derivation. *Pulsellum salishorum* may also have a defined adult size, although this is less clear (Table 7).

For the *Dentalium* and *Pulsellum* specimens, LWm = 0, and Wm = ApW + 2(shell thickness). These values alone separate these individuals from the adult *Cadulus* specimens, although as discussed above, juvenile *Cadulus aberrans* also show the same values.

Dentalium rectius, on the other hand, obviously grows in an indeterminate manner. The large variance in the total length measurements confirms this, as does the substantial number of healed fractures at various points along the shell (unpublished observations).

The shell morphology indices used here are consistent and useful as objective measures of shape. Coupled with clustering analysis they allow the discrimination of subtle adult shell shape differences. Even the very similar morphologies of the slender Gadilida are separated. Consequently, I conclude that these measurements show the morphological limits to four species of slender gadilid scaphopods (Table 7).

Pulsellum salishorum was obviously the easiest of the northeastern Pacific Gadilida to discriminate. There was never any apertural narrowing, and the shell surface texture was decidedly different, being unpolished and similar to that of *Dentalium.*

The other gadilid species are similar in shell surface texture and general shape. Nonetheless, use of the length (LI) and width (WI) indices and the rate of whorl expansion (Ws) can adequately separate them. The length and width indices are usually significantly different among these species and show quite small within-species variances even though the populations examined might be geographically distant. The whorl expansion rate is more variable, and consequently less useful on its own as a discriminating agent. This variability is likely due to the animals' small size and the resultant measurement errors. These errors, although individually minute, are magnified in the calculation process, producing substantial index variations. Similarly, because of the calculation methods for Ws, slight variations in the initial curvature of the shell will introduce large variations in this index. Even so, use of Ws alone is sufficient to discriminate among some of the species. The

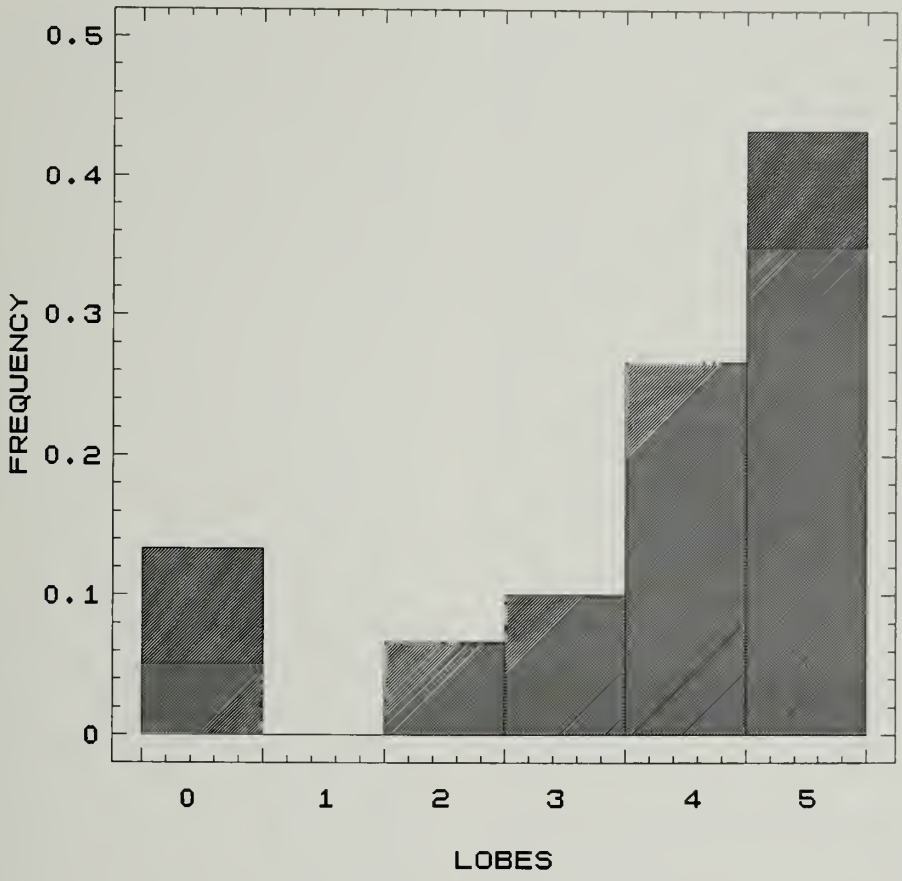

Figure 5

Cadulus tolmiei dorsal apertural lobes. $n = 30$. All specimens collected from 48.89°N, 125.05°W, 150–350 m depth.

three indices together allowed the determination of three superficially similar species of slender gadilid scaphopods from within the pool of specimens examined.

Because the measurements leading to these indices are simple, replicable, and unambiguous, the use of the indices in comparative studies can allow rapid separation of similar shell morphologies in animals such as scaphopods where only subtle shell shape differences separate distinct species. In the case of an unknown shell similar to the species examined here, the comparison of the calculated length and width indices with the ranges published here would tell whether that shell was of similar shape. Examination of the other meristic data (*i.e.*, length, width, maximal arc) would confirm or deny the existence of shape congruity. For fossils, these data might be sufficient to identify the shell. Other aspects of the biology of the living animals should certainly be examined before the identification was confirmed, but the removal of the ambiguity in the description of shell shape should certainly assist in the identification process.

The smallest of the three inferred groupings, containing those animals collected from 23.52°N and 29°N, was concluded to be *Siphonodentalium quadrifissatum* (Pilsbry & Sharp, 1898). This group often showed more overlap with the southern populations of *Cadulus* than the northern ones; nevertheless, the differences in the index means were significant. Although none of the five animals from the 29°N population possessed the lobulation of the narrow aperture characteristic of this species, virtually all specimens examined from the 23.52°N population had these apertural lobes and all specimens were similar in other characteristics. The lobulation of the posterior aperture was quite variable in *Cadulus tolmiei* (Figure 5), and I suspect the lack of the lobulation in the sample from the 29°N population simply reflected the small sample size. Although I did not examine the type of *S. quadrifissatum*, the shells examined here closely match the original descriptions of that species (Pilsbry & Sharp, 1897–1898).

The other species were superficially similar in general morphology: they were small, seldom more than 13 mm long, slender, and rarely over 1.5 mm wide; they lacked lobes around the dorsal aperture, and were slightly curved. They differed, however, in the distance from the ventral aperture to the point of greatest width (LI), and in the

amount of constriction of the ventral aperture (WI). Furthermore, although there was a range of geographical overlap, the different morphologies remained distinct throughout the range of overlap. One species was found in the northeastern Pacific, and its southernmost limit was from central to southern California. The other was found from the same latitudinal area south.

This southern species is concluded to be *Cadulus perpusillus*. The general morphology of the examined specimens is similar to descriptions and photographs of that species (KEEN, 1971; EMERSON, 1971); however, a photograph of the lectotype (EMERSON, 1971) yielded measurements and indices somewhat different from those in the populations studied herein (Table 1). *Cadulus perpusillus* has a range extending substantially to the south of the populations I examined (EMERSON, 1971; KEEN, 1971), and the type is from these more southern populations. It is certainly possible that the examined specimens from the northern populations were less variable than the species as a whole, or that their measurements were skewed in some manner relative to the rest of the species.

The northern species was first described by WHITEAVES in 1887, from specimens collected in Quatsino Sound on the northwestern edge of Vancouver Island (Table 1). Several other similar nominal species were subsequently described. Examination and measurement of the types of *Cadulus fusiformis, C. hepburni,* and *C. nitentior* show, however, that these species are junior synonyms of *C. aberrans*. The analyses herein show conclusively that *C. fusiformis* has a shell morphology consistent with *C. aberrans,* and is thus a junior synonym of that species (Table 1). The similar close correspondence in the shapes for the type specimens also shows that *C. hepburni* is also a junior synonym and confirms the opinion (GRANT & GALE, 1931) that *C. nitentior* is too (Table 1).

Interestingly, none of the described types is a "typical" *Cadulus aberrans,* if "typical" is defined as having the average characteristics of the species. The indices derived from measurements of all of the types are displaced substantially from the centers of the distributions of any of the indices. Nonetheless, they are clearly within the range of variation of those species.

The indices also differentiated more distinctly different *Cadulus* species, for example, *C. tolmiei*. Although the variances around the index means were greater for this species than those around the means for any of the slender species, the indices together still served to delimit them all (Table 7). Insignificant differences among the various parameters point out some hitherto undiscerned correspondences in shape, however, such as the relative degree of aperture narrowing that is similar in *C. tolmiei* and *Siphonodentalium*.

Functionality of Shape

All *Cadulus* are narrower around the ventral aperture than around the middle portion of the shell. Indeed, this characteristic is the major morphological shell character delimiting this genus. Nevertheless, no function has been proposed for the narrowing of the aperture. This study shows that at least *C. aberrans* (and *C. tolmiei*) juveniles do not have the narrowed aperture. Consequently, these animals are clearly able to live and grow having two different morphologies. Indeed, a strict interpretation of the generic characters of shell shape alone would assign the juveniles to a different genus.

Natural history observations may allow the determination of a selective advantage to the narrowed aperture. These animals prey upon foraminiferans collected from the surrounding sediment. Items that may be eaten are brought into the mantle cavity where they are manipulated prior to being eaten (SHIMEK, 1988). Both juveniles and adults, however, eat the same types of prey. Furthermore, the adults, even with the narrowed aperture, eat larger prey than do the juveniles. Thus it seems unlikely that the narrowing of the aperture has any relation to the kind or size of the prey eaten.

In addition to narrowed apertures, all live, and recently dead, *Cadulus* that I examined also had highly polished shells. They were very slippery and difficult to grasp. Furthermore, *C. aberrans* is quite capable of rapid locomotion (up to 1 cm/sec) through the sediment in which it is normally found (Shimek, unpublished observations).

In the laboratory, I have maintained *Cadulus aberrans* for several months in sediment taken from their natural habitat. During this period I observed them regularly, and seldom saw them with the dorsal aperture extended into the water column. In many cases I watched them through the sides of their glass or transparent plastic containers. Contrary to the information normally given about scaphopods, these animals seldom got closer to the surface than 6–8 cm and were commonly found buried as deeply as 30 cm. During reproduction, however, they must be close enough to the surface to be able to liberate their gametes directly into the water. During this period, sexually mature adult *C. aberrans* would be subject to predation by epibenthic predators.

Although I lack direct evidence, I suspect that adult *Cadulus aberrans* individuals with a narrowed aperture can burrow faster than juveniles of the same length. I suggest that the narrowing of the aperture of *Cadulus* species has evolved, together with the highly polished shell, in part to permit rapid, efficient, burrowing to escape predation. As a corollary to this, it follows that juveniles would tend to be found deeper in the sediments than the adults, which would account for their relative rarity in collections. The highly polished shell may also make it difficult for a predator to seize a *Cadulus* individual.

Dentalium rectius and *Pulsellum salishorum* are often sympatric with *Cadulus aberrans* or *C. tolmiei,* and both of the former species often show healed shell fractures (Shimek, unpublished data), presumably caused by attempted predation. Such healed fractures are rare on *C. aberrans,* indicating little unsuccessful predation, and perhaps indicating success by the scaphopod at escaping predation.

In the Barkley Sound region, the major predators on

scaphopods are ratfish, *Hydrolagus colliei* (Shimek, in prep.). During examination of *H. colliei* gut contents I commonly found *Dentalium rectius* and *Pulsellum salishorum,* while *Cadulus* species were seldom noted, even though the fishes were collected from habitats where *Cadulus* is common. Similarly, longsnout pricklebacks, *Lumpenella longirostra,* which live below depths of 250 m in some soft-sediment Alaskan habitats, are predators on small mollusks. Their guts often contain only *P. salishorum* even though both *P. salishorum* and *C. tolmiei* are common in those areas (Baxter, personal communication).

Shell Character Sets in Scaphopods

Species and generic determinations in scaphopods have been dominated by differences in shell shapes with little or secondary regard to the morphology of the body secreting the shell (Pilsbry & Sharp, 1897–1898; Ludbrook, 1960; Habe, 1963, 1964; Shimansky, 1963; Starobogatov, 1974; Palmer, 1974; Chistikov, 1975; Emerson, 1952, 1962, 1978). In some cases, these shell characters appear to have been applied arbitrarily, without any consideration of variability, and have been used to erect higher-level systematic groupings that therefore may be spurious (Dall, 1897; Pilsbry & Sharp, 1897–1898; Carter, 1983).

The reasons for the uncritical use of variable shell characters in scaphopods are probably related to the lack of easily defined shell character sets within the class. At first glance, the scaphopod shell seems featureless, and the need to discriminate between perceived species has fostered the use of minute, subjective, and variable shell characters. This study indicates that quantification and manipulation of only a few measurements can be used to assess variability and accurately determine similar shell shapes. Thus the use of variable characters is unnecessary; in effect, the shell is not as featureless as it may seem.

Additionally, the lack of population and ecological information has contributed to the use of characters that are simply either expressions of variability within the population or phenotypic responses to ecological events. For example, *Dentalium rectius* collected from Barkley Sound often has the tip of the dorsal aperture broken off. This occurs as the result of breakage or attempted predation by the ratfish, *Hydrolagus colliei,* which nips the tip off (if it does not eat the whole animal). As a result, during subsequent shell repair, a secondary tube is secreted from the dorsal aperture. This tube is effectively identical with those illustrated by Emerson (1962) and Palmer (1974) as a character for the genus *Episiphon* Pilsbry & Sharp, 1897, although Emerson (1962) also illustrates several other genera with a similar tube. The growth of this tube in *D. rectius* is rapid; I have measured tubes of 10 mm or more in length secreted by an adult within 2–3 weeks in the laboratory. This particular morphology, at least within *D. rectius,* indicates nothing other than shell repair. I suggest that similar morphologies in other species indicate similar processes of either shell repair or growth. Unless these changes in shape can be shown to be correlated with differences in internal morphology distinct from other populations lacking the morphological attribute in question, they certainly should not be used for generic discrimination, although they may be useful as indicators of potential predation pressure.

The lobation of the dorsal aperture also deserves particular mention as it has been used as the primary character to discriminate subgeneric (or, more recently, generic) groupings within *Cadulus* Philippi, 1844 (Palmer, 1974; Scarabino, 1979; Carter, 1983). The data presented on *C. tolmiei* (Figure 5) clearly show this character to be variable within a single well-defined population of a geographically widespread species. The genera *Polyschides* Pilsbry & Sharp, 1898, and *Platyschides* Henderson, 1920, have been defined, in part, on the basis of the number of slits between the lobes and their relative depth even though the latter likely depends upon relative growth rates. Without addressing the variability, both within and between species, uncritical acceptance of these genera is not warranted.

Critical examination of the variability of shell characters may validate existing subgeneric groupings as well. These slender *Cadulus* can be or have been placed in the subgenus *Gadila* Gray, 1847. If examination of other aspects of the anatomy indicates that this is a natural group distinct from the more typical *Cadulus,* then generic status would be warranted. Until that time it seems prudent to maintain these species within *Cadulus.* Interestingly, given the ambiguity concerning the validity of *Polyschides* and *Platyschides, Gadila* may be the only presently named valid subgeneric unit in *Cadulus.* Elaboration of these indices might present a way to subdivide critically this genus on the basis of shell shape; corroborative studies of the other aspects of the anatomy could then be used to confirm these subdivisions.

One major reason for the subdivision of *Cadulus* into several genera seems to be the impression that a large genus is somehow unwieldy and not useful (Palmer, 1974). On the contrary, if a given morphology is successful and becomes widespread, then maintaining similar, and obviously closely related, species of common descent together in one natural genus allows a reasonable evaluation of the factors contributing to the success of that body plan. Examination of closely related, similar morphologies has been used to advantage within many of the larger genera of mollusks, *i.e., Buccinum, Conus, Macoma, Murex, Octopus, Oenopota,* and *Terebra,* and certainly could be used within this relatively small class.

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Chromodorid Nudibranchs from the Hawaiian Islands

by

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Abstract. We propose four new specific taxa of Opisthobranchia—*Hypselodoris* ***andersoni***, *Glossodoris* ***poliahu***, *Glossodoris* ***tomsmithi***, and *Ardeadoris* ***scottjohnsoni***—and we redescribe *Chromodoris albopunctata* (Garrett, 1879). We comment on the anatomy, ecology, and zoogeography of these species, and interspecific differences with their Indo-Pacific congeners.

INTRODUCTION

Although the molluscan fauna of the Hawaiian Islands is one of the best known among the western and central Pacific islands, knowledge of the opisthobranch species is far from complete (GOSLINER *et al.*, 1986). These authors recently wrote that they are aware of over 90 undescribed species of opisthobranchs that occur in this island archipelago.

In our previous studies, we have discussed the zoogeography and taxonomy of various cephalaspidean, doridacean (BERTSCH & JOHNSON, 1979, 1982), dendronotacean (GOSLINER, 1987a), and eolidacean (GOSLINER, 1980) species of Hawaiian opisthobranchs. In this paper, we describe four new species of doridacean nudibranchs from the Hawaiian Islands and correct the nomenclature of another species. Two of these have been previously listed as unnamed species ("locust" and "snowflake" of BERTSCH & JOHNSON, 1981), and three were originally misidentified in Hawaiian waters as *Chromodoris imperialis* (*non* Pease, 1860), *Chromodoris albonotata* (*non* Bergh, 1875), and *Chromodoris sibogae* (*non* Bergh, 1905) (by KAY & YOUNG, 1969; KAY, 1979; and BERTSCH & JOHNSON, 1981). All five of these species are illustrated with color photographs in BERTSCH & JOHNSON (1981).

Collecting localities from the Hawaiian island of Oahu are identified in Figure 1; approximate coordinates for sites from other central Pacific islands are given in the text.

Family CHROMODORIDIDAE

Hypselodoris Stimpson, 1855

Hypselodoris ***andersoni*** Bertsch & Gosliner, sp. nov.

(Figures 2, 7–12)

References:
Locusts: BERTSCH & JOHNSON, 1981:66–67, 107 (color photographs).
Chromodorid 1: JOHNSON, 1983:356–364.

Material examined: (1) Holotype, California Academy of Sciences, CASIZ 064807; collected subtidally, 5 m depth, Pupukea, Oahu, 11 September 1987, Terrence M. Gosliner (TMG).

(2) 2 paratypes, California Academy of Sciences, CASIZ 064820; collected subtidally, 10 m, past Makua, Oahu, 15 September 1978, by Scott Johnson (SJ) and Hans Bertsch (HB) (*ex* HB 710).

(3) 1 dissected paratype, CASIZ 066609; collected subtidally, 10 m, past Makua, Oahu, 15 September 1978, SJ and HB.

(4) 11 paratypes, CASIZ 064808; same locality and date as holotype.

(5) 1 dissected paratype, CASIZ 066608; same locality and date as holotype.

(6) 1 paratype, CASIZ 064809; collected subtidally, 10 m, Makua, Oahu, 14 September 1987, TMG.

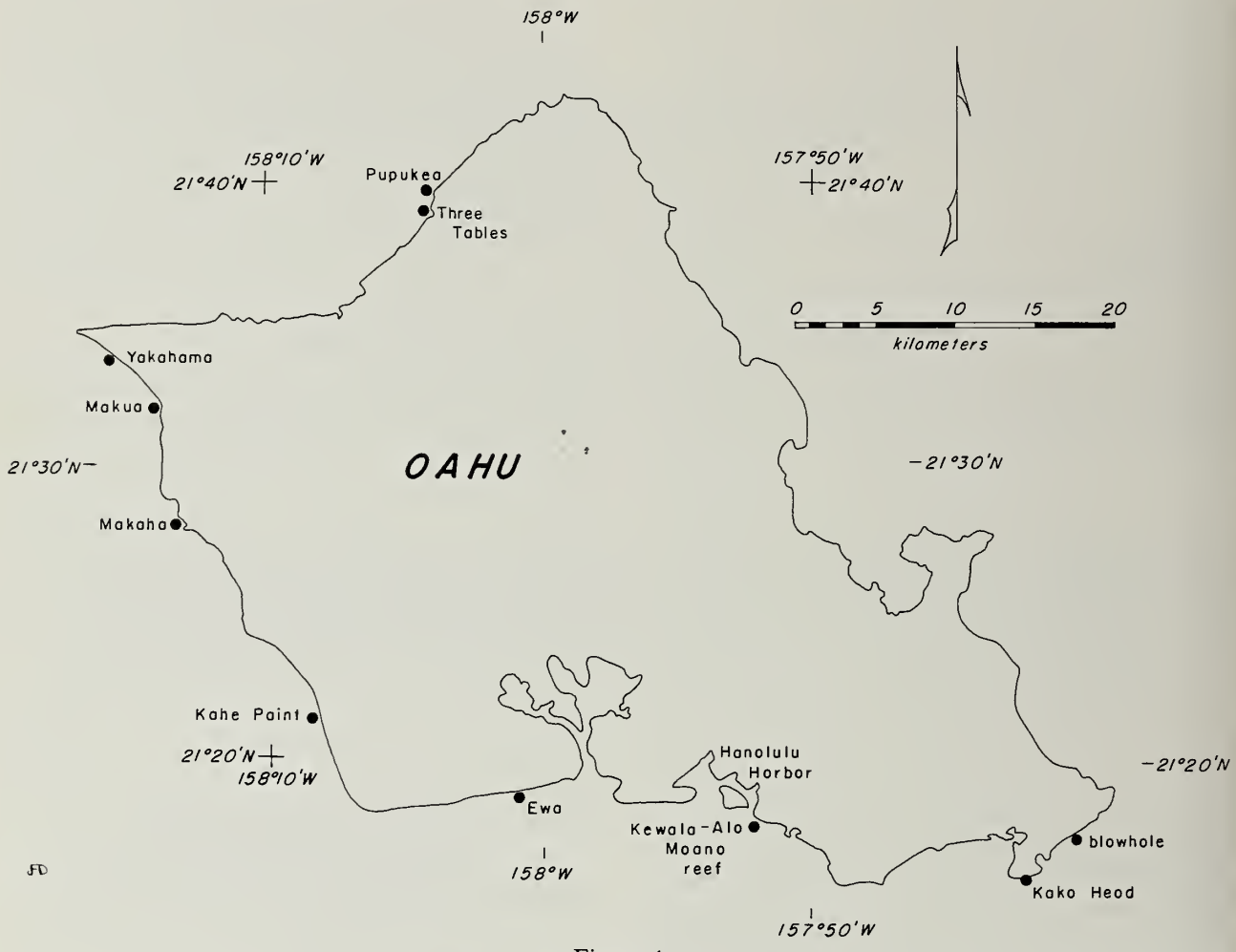

Figure 1

Map of Oahu, showing collecting localities.

(7) 5 paratypes, Los Angeles County Museum of Natural History, LACM 2294; collected subtidally, 15 m, at Pupukea, Oahu, 18 September 1978, SJ (*ex* HB 718).

(8) 1 specimen, collected subtidally, 17 m, off the Lanai Lookout, Oahu, 26 September 1978, SJ (*ex* HB 733).

(9) Additional specimens reported from the western shore of Oahu near Makua by JOHNSON (1983).

Distribution: Specimens of *Hypselodoris* ***andersoni*** have been collected from high-energy, rocky subtidal regions on the east, west, and north shores of Oahu, to 18 m deep.

Etymology: This species is named in honor of our good friend and colleague Mr. Roland Anderson of the Seattle Aquarium. We especially salute his untiring efforts and enthusiasm at educating the public regarding the biology and beauty of living mollusks.

External morphology: Preserved specimens measure about 3–7 mm in total length; living animals can reach 15 mm long, but the monthly averages for several hundred animals ranged from about 4 to 7 mm (JOHNSON, 1983:fig. 4).

The animals are elongate, with the posterior portion of the foot protruding slightly behind the dorsum (Figure 2). The mantle margin forms a very small ridge; since there is almost no rim hanging over the side of the foot, the foot sides are completely exposed (characteristic of species of *Hypselodoris*; cf. RUDMAN, 1984:185). The rhinophores and gills are set at the far extremes of the body; rhinophores are cream white to pink with an encircling red-orange band about two-thirds of the distance to the tip. The 6–8

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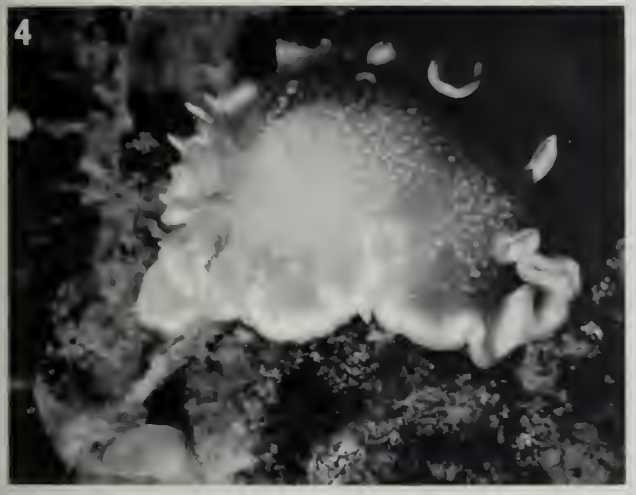
Explanation of Figures 2 to 6

Figure 2. *Hypselodoris* ***andersoni*** sp. nov.: *in situ* photograph of 8- and 10-mm-long animals on prey sponge; photo by Scott Johnson, 5 m underwater, Makua, Oahu, December 1977.

Figure 3. Close-up of *Chromodoris albopunctata* (Garrett, 1879):



50-mm-long animal collected at Magic Island, Oahu; photo by Hans Bertsch, 11 May 1978.

Figure 4. *Glossodoris* ***poliahu*** sp. nov.: 25-mm-long animal; *in situ* underwater photo by Hans Bertsch, 10 m deep, Three Tables, Oahu, 6 August 1981.

Figure 5. *Glossodoris* ***tomsmithi*** sp. nov.: 24-mm-long animal; *in situ* underwater photo by Hans Bertsch; 12 m deep, Makua, Oahu, 15 July 1980.

Figure 6. *Ardeadoris* ***scottjohnsoni*** sp. nov.: 21-mm-long animal; underwater photo by Scott Johnson, Puako, Hawaii, May 1978.

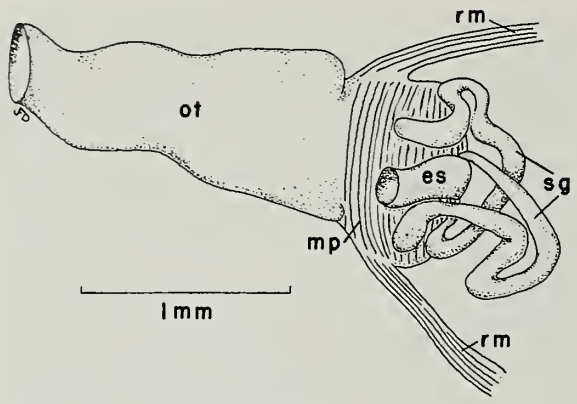


Figure 7

Hypselodoris ***andersoni*** sp. nov. Dorsal view of the foregut of specimen CASIZ 066608. Symbols: es, esophagus; mp, muscular portion; ot, oral tube; rm, retractor muscle; sg, salivary gland. Scale = 1 mm.

simply pinnate gills are held erect, closely together, with the distal tips curling in towards the center of the gill circlet. They are basally and distally cream colored, with most of the gill possessing a red-orange coloration, especially on the outer face.

The dorsum and sides of the foot are cream colored to pink; the mantle margin is usually tinged with a continuous deep blue band encircling the whole animal (less frequently there are slight interruptions of this band; even when the band is not continuous the appearance is of a solid line, not a broken one), and another blue band around the rim of the foot (most prominent on the posteriorly protruding part of the foot). The dorsum is streaked with 10–12 thin, opaque white, nearly parallel, close-set longitudinal lines, some of which may be discontinuous.

Buccal mass and radula: The buccal apparatus is well developed (Figure 7). The oral tube is elongate with an apparently glandular epithelium. At the junction of the oral tube and the muscular buccal mass is a pair of long retractor muscles. The muscular portion consists largely of circular bands of muscle, and contains the jaws and radula. The esophagus recurves anteriorly on the dorsal surface of the buccal mass. On each side of the esophagus is the insertion of the duct of an elongate salivary gland.

The radular formula of a specimen collected at the Lanai Lookout was 40 × 34·0·34, and a paratype from Pupukea had a formula of 53 × 38·0·38 (counted from scanning electron micrographs). The innermost lateral teeth (Figure 8) have a prominent denticle on the inner side of the erect shaft, and 1–3 denticles below the main cusp. Lateral teeth are bicuspid (lacking inner denticles); middle lateral teeth have 1 or 2 denticles below the bifid cusp; outermost lateral teeth (Figure 9) have 3–5 denticles below the main cusps, and become stubbier in appearance. Jaw armature (Figures 10, 11) consists of simple or bifid hooks.

Reproductive system: The arrangement of the reproductive system is triaulic (Figure 12). The pre-ampullary duct expands into a straight ampulla. The ampulla divides distally into a short oviduct and the prostatic portion of the vas deferens. The vas deferens is highly convoluted throughout most of its length. Distally it widens into a straight ejaculatory segment, prior to entering the penial sac. The oviduct enters the female gland mass. Adjacent to the entrance of the oviduct into the female gland mass is the narrower uterine duct. The uterine duct joins the vagina near the minute receptaculum seminis. The spherical, thin-walled bursa copulatrix is located at the proximal end of the vagina. A large, digitate vestibular gland joins the female gland mass, vagina, and penis at the common genital aperture.

Natural history: The biology of this species was studied by JOHNSON (1983). He described its predation exclusively on the sponge *Luffariella* sp. (also illustrated in BERTSCH & JOHNSON, 1981:66, 107), its density and distribution in relation to its prey sponge, monthly variation in body length, and its year round reproductive cycle and laying of egg masses (illustrated in BERTSCH & JOHNSON, 1981:66).

Discussion: This new species is most similar to the Hawaiian specimens attributed to *Hypselodoris lineata* (Eydoux & Souleyet, 1852) by OSTERGAARD (1955), KAY & YOUNG (1969), and BERTSCH & JOHNSON (1981). However, EYDOUX & SOULEYET's (1852) species has purple rather than white longitudinal lines. That species is probably synonymous with *H. maridadilus* (Rudman, personal communication). However, *Doris lineata* Eydoux & Souleyet, 1852, is a primary homonym of *Doris lineata* Brocchi, 1819. Therefore, *H. maridadilus* remains the valid name for the species. The Hawaiian specimens represent an undescribed species that we distinguish from *H.* ***andersoni***. The living animals are immediately separable. *Hypselodoris* ***andersoni*** tends to be smaller (<15 mm) than *H.* sp.; the white lines on the dorsum are more numerous and often extend the full length of the animal's dorsum; the gills and rhinophores have a lighter golden yellowish hue; the blue band around the mantle is complete and a light-toned bluish color; and there are no prominent navy blue streaks or splashes of color on the central region of the dorsum. *Hypselodoris* sp. (see color photo in BERTSCH & JOHNSON, 1981:65) is larger (20–30 mm) and has about 5–8 frosty

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Explanation of Figures 8 to 11

Figures 8–11. Scanning electron micrographs of the radula and jaws of *Hypselodoris* ***andersoni*** sp. nov. Illustrated specimen is CASIZ 066608.

Figure 8. Innermost teeth of radula.

Figure 9. Teeth near middle of half-row of radula.

Figure 10. Jaw elements.

Figure 11. Close-up of jaw armature.

8
101912 15KV X1.70K 17.6um

9
101913 15KV X2.00K 15.0um

10
101911 15KV X800 38um

11
101910 15KV X2.50K 12.0um

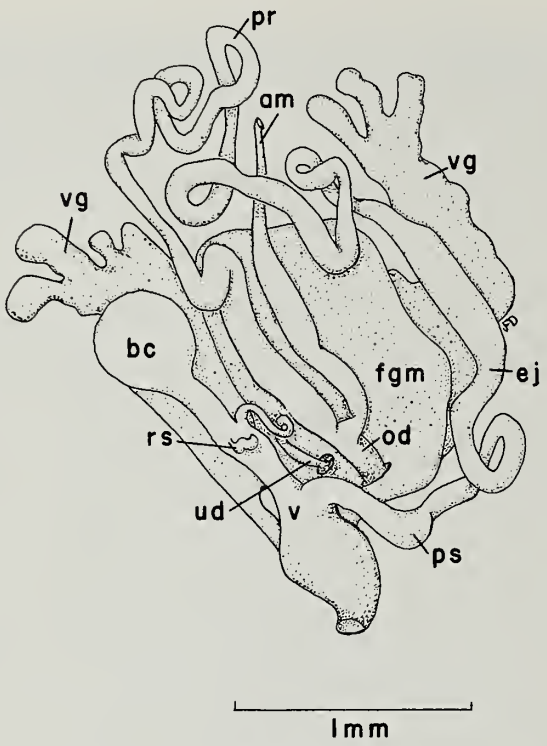

Figure 12

Reproductive system of *Hypselodoris* ***andersoni*** sp. nov. Illustrated specimen is CASIZ 066609. Symbols: am, ampulla; bc, bursa copulatrix; ej, ejaculatory portion of the vas deferens; fgm, female gland mass; od, oviduct; pr, prostatic portion of vas deferens; ps, penial sac; rs, receptaculum seminis; ud, uterine duct; v, vagina; vg, vestibular gland. Scale = 1 mm.

Figure 13

Drawing of radular teeth of *Chromodoris albopunctata.*

white lines on the dorsum that merge, anastomose, and are interrupted at various places on the back; there is a dark yellow-orange coloring on the rhinophores and gills; the mantle is margined with a thin, opaque white line, inside of which is a broken (interrupted) band of navy blue; there are also numerous dark navy blue streaks and splashes of color extending lengthwise in irregular rows down the animal's back. *Hypselodoris* ***andersoni*** has 6 gills, and *H.* sp. has 10–12 gills.

Internal morphological differences are seen in the radula and reproductive system. The innermost lateral teeth of *Hypselodoris* sp. lack denticles other than the bifid cusp (Kay & Young, 1969:209). The reproductive system of *H.* sp. (as shown by Kay & Young, 1969) differs from that of *H.* ***andersoni*** in that the vas deferens is thicker and less convoluted.

There are also ecological differences. *Hypselodoris* sp. tends to be a solitary, intertidal species, whereas *H.* ***andersoni*** often feeds in aggregations of more than two or three individuals (Johnson, 1983:363) and is subtidal in occurrence.

At least four other species of *Hypselodoris* have opaque white longitudinal lines on the notum. *Hypselodoris macculosa* (Pease, 1871) has a more complex color pattern with submarginal red-orange pigment and scattered purple spots on the notum. Its radular teeth bear more denticles than do those of *H.* ***andersoni***. The vaginal duct is much shorter in *H. maculosa* (Rudman, 1986b) than in *H.* ***andersoni***. *Hypselodoris capensis* (Barnard, 1927) and *H. carnea* (Bergh, 1889) both have black or dark brown spots on the notum (Gosliner, 1987b). *Hypselodoris capensis* has denticles only on the outer 5 or 6 radular teeth while all of the teeth are denticulate in *H.* ***andersoni***. *Hypselodoris carnea* has a rachidian tooth, which is absent in *H.* ***andersoni***. Gosliner (1987b) reported an additional species with white lines (*H.* sp. 1). It also has red longitudinal lines paralleling the white lines, and yellow and purple marginal rings. This species has denticles on only the outer 10–12 radular teeth.

We are aware of the similarities of our new species with *Doris prismatica* var. *lineata* Pease, 1860, and two unde-

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Explanation of Figures 14 to 17

Figures 14–17. Scanning electron micrographs of the radula and jaws of *Chromodoris albopunctata.* Illustrated specimen is CASIZ 066610.

Figure 14. Rachidian and inner lateral teeth.

Figure 15. Radular teeth from middle of half-row.

Figure 16. Outer lateral teeth.

Figure 17. Jaw elements.

1
060911 15KV X1.20K 25.0um

15
060912 15KV X1.50K 20.0um

16
060913 15KV X1.00K 30um

17
060910 15KV X2.00K 15.0um

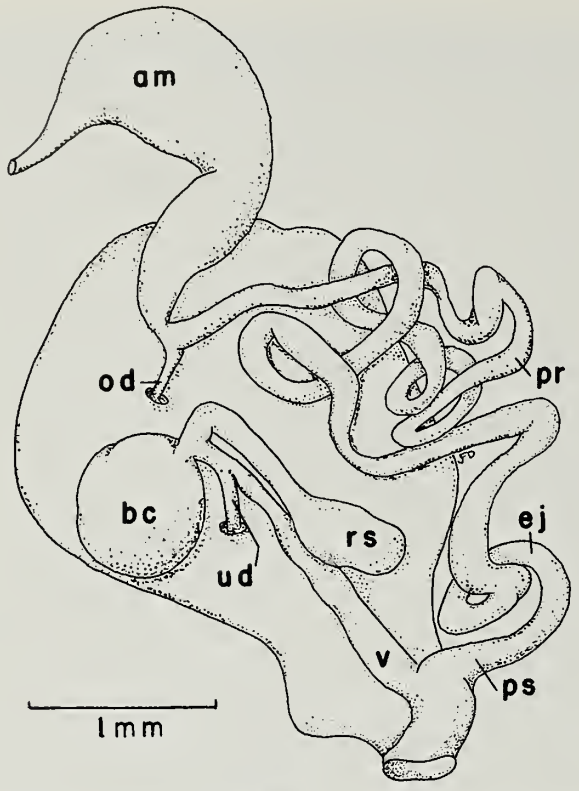

Figure 18

Reproductive system of *Chromodoris albopunctata*. Illustrated specimen is CASIZ 066610. Lettering symbols as in Figure 12. Scale = 1 mm.

scribed species of *Hypselodoris* (including "white dot," illustrated in BERTSCH & JOHNSON, 1981:66) from the Hawaiian Islands. It is difficult to identify Pease's species, because his description is vague and lacks information on the internal anatomy of the animal. Nevertheless, Pease's species is a junior homonym of both Brocchi's and Eydoux & Souleyet's *lineata* species, so it would require a new name.

Chromodoris Alder & Hancock, 1855

Chromodoris albopunctata (Garrett, 1879)

(Figures 3, 13–18)

References and synonymy:

Goniodoris albopunctatus GARRETT, 1879:31.

Chromodoris albopunctatus [sic]: JOHNSON & BOUCHER, 1984:263–264.

Chromodoris imperialis (*non* Pease, 1860): KAY & YOUNG, 1969:202, figs. 41, 59; KAY, 1979:467, 469; BERTSCH & JOHNSON, 1980; BERTSCH & JOHNSON, 1981:48–49, 58–59 (color photographs). *Chromodoris imperialis* (Pease, 1860) is actually *Risbecia imperialis* (Pease), and *Chromodoris godeffroyana* Bergh, 1877a, appears to be a junior synonym, based on specimens collected in Tahiti, the type locality of the latter species (*cf.* Bertsch, in prep., and personal observation).

It is unclear whether specimens identified as *R. godeffroyana* by RUDMAN (1984) and WILLAN & COLEMAN (1984) are also conspecific, or whether they represent an undescribed species.

Material examined: (1) 3 specimens, CASIZ 064821; collected subtidally, 3 m, at Ewa, Oahu, 29 June 1978; Stan Jazwinski (*ex* HB 756).

(2) 1 dissected specimen, CASIZ 066610; from the Ewa site, 29 June 1978.

(3) LACM 78-183; 2 specimens, collected subtidally, 5 m, Honolulu Harbor, Oahu, 2 July 1978; Stan Jazwinski (*ex* HB 776).

(4) Additional specimens from Kewalo (straight off Ala Moana Reef), Oahu, August 1977; SJ (illustrated in BERTSCH & JOHNSON, 1981:48, upper right).

(5) 1 specimen, collected at night, subtidally, 12 m, at west side of Savo Island, Solomon Islands (9°8′S, 159°47′E; approximately 5400 km SW of Oahu), 20 August 1977; Jeanette Johnson (personal communication, Scott Johnson).

Distribution: The infrequent Hawaiian records of this foudroyant, colorful species are all from Oahu. However, this species was originally described from Huahine, Society Islands (approx. 16°45′S, 151°00′W), over 4000 km S of Oahu. It has also been reported from Enewetak Atoll (approximately 11°20′N, 162°20′E), more than 3500 km SSW of Oahu (JOHNSON & BOUCHER, 1984:263–264). These records (including our new report from the Solomon Islands) indicate a wide range through the central tropical Pacific.

External morphology: Preserved specimens measure 15–20 mm in total length; living animals longer, usually from 20 to 45 mm long, although KAY (1979) reported a specimen 65 mm long.

General body shape oval (Figure 3), low in profile (flattened dorsoventrally). Mantle completely overhangs the sides of the body, covering the foot. Mantle margin smooth, may be temporarily ruffled as it is lifted or moved by the animal.

Rhinophores darkish red-brown, with interrupted white streaks, dots, or dashes on the edges of the 21–35 lamellae, and a vertical white line down the center. The 8–10 gills are often retracted; expanded they are elongate, and encircle the anal opening. They are the same color as the rhinophores (KAY, 1979:469, fig. 150H).

Central portion of the dorsum light red, on which are numerous opaque white rings. Around the perimeter is an inner golden yellow-orange band, surrounded by an outer blue band (this blue band tends to be darker on the inside and lighter on the outside). Between the red and white ringed central dorsal region and the yellow band, the white coloration coalesces into splashes and patches, forming an interrupted boundary region.

The foot is a uniform golden orange (same as the band between the blue and red-white portions of the dorsum), with no other colors forming a margin to the foot.

Some color variation was observed in the animals we studied. A 14-mm-long specimen found in 15 m depth at Makua, Oahu, had a dorsum totally of golden yellow, with white rings. Instead of the reddish central dorsal coloration, the color of the circumferential golden yellow band continued throughout the entire dorsum. The specimen found at Enewetak was similar in all coloration shades and tones to the more typical animals collected at Hawaii. However, the blue and gold bands around the perimeter were a bit narrower than usual for the Hawaiian specimens. A light blue, dark blue, and an inner yellow band form a characteristic marginal color pattern for this species.

Buccal mass and radula: The buccal apparatus is muscular throughout most of its length. There is no distinct, elongate oral tube. KAY & YOUNG (1969) reported a radular count of 63 (65·0·65). Contrary to their description, a small rachidian tooth is present (Figure 14). The specimen illustrated with SEMs (Figures 14–17) has a count of 49 × 41·1·41. Another specimen we dissected had 49 rows and 53 teeth per half-row. The minute rachis was visible even with light microscopy. The innermost lateral tooth has 3 or 4 inner lateral denticles and 4–6 outer lateral denticles (Figures 13, 14). Lateral teeth from the middle of each half-row (Figure 15) have 8–12 posterolateral denticles on the erect cusp. The outermost lateral teeth (Figure 16) become shorter and wider (along the anteroposterior plane). Jaw structure elements are simple, or with a small accessory tip below the main tip, making most elements bifid (Figure 17). Line drawings of the radular teeth and elements of the jaw armature are presented in KAY & YOUNG (1969:201, fig. 41B, C).

Reproductive system: The ampulla (Figure 18) is large and saccate, consisting of several convolutions. Distally, it narrows and divides into the short oviduct and elongate, convoluted vas deferens. The proximal portion of the vas deferens is prostatic and distally it forms a muscular, ejaculatory segment. The penial sac is slightly expanded and contains minute penial rodlets. The uterine duct is short and straight, and enters the vagina immediately distal to the junction of the spherical bursa copulatrix and the recurved, pyriform receptaculum seminis. The vagina is long and straight.

Our diagram (Figure 18) compares well with that of KAY & YOUNG (1969:201, fig. 41A), with the exception that theirs is an "exploded" illustration, with the various sections of the system pulled apart.

Discussion: Most features of GARRETT's (1879) terse external description closely match the characters of our Hawaiian specimens: "The upper surface is bright orange-yellow, with crowded opaque white dots, and minute annulae; the mantle with a band of small irregular lemon-yellow spots near the margin, which latter is edged with violaceous. . . . The dorsal tentacles . . . [rhinophores] purple-brown, profusely dotted with opaque white, and marked with two vertical lines of the latter color. The branchial plumes . . . are colored and dotted similar to the tentacles, and each ornamented with two longitudinal white lines. The under surface of the mantle and foot are pale lemon-yellow, the former margined the same as above." The only discrepancy is that our specimens had a solid yellow band inside the violet marginal band, not a band of irregular lemon-yellow spots. Connected spots versus a solid band is certainly just an example of intraspecific variation in dorid coloration patterns. Moreover, KAY & YOUNG's (1969: 212, fig. 59) illustration (reprinted in KAY, 1979:469, fig. 150H) shows a nearly continuous yellow marginal band, with several interrupting gaps.

External features immediately distinguish *Chromodoris albopunctata* from *Risbecia imperialis* (Pease, 1860). Pease's species has a white body with golden yellow dorsal spots, and a single dark navy blue marginal band, with a varying number of medially pointed navy blue flanges in which are 0–4 yellow dots (*cf.* illustrations in BERTSCH & JOHNSON, 1981:50–51).

Several other species have a similar reddish and white maculation to the dorsum, but they do not have the distinctive yellow and blue marginal bands. In the cases of all the other species with red and white reticulation, the ground color is white overlain with red. However, in *Chromodoris albopunctata* the ground color is reddish with opaque white pigment deposited on top of the red. *Chromodoris petechialis* (Gould, 1852) has a faint yellow margin and light yellow orange rhinophores; *Chromodoris tinctoria* (Rüppell & Leuckart, 1828) has red reticulations on the mantle, but the rhinophores are gray and the gills are translucent (WILLAN & COLEMAN, 1984:22–23), there is no marginal banding of yellow and blue, and the body shape is different from *Chromodoris albopunctata*. *Glossodoris gregorius* Rudman, 1986a, has white spots, but they are less pronounced than in *C. albopunctata,* and do not form rings; the dorsum of *G. gregorius* is a darker reddish brown, rather than bright orange red. This species has two marginal bands: an outer black and an inner yellow. The radula and other internal characteristics also distinguish the two species (hence their placement in two different genera).

Two species of *Chromodoris* have blue or violet outer marginal bands. JOHNSON & BOUCHER (1984) considered *Chromodoris sykesi* Eliot, 1904, to be a synonym of *C. albopunctata,* but we consider it premature to synonymize these species until *C. sykesi* from the type locality can be re-examined. Although very similar in coloration, there are several intriguing differences: the branchial pocket of *C. sykesi* was described as a "capacious and very strong bag," the rhinophore perfoliations were indistinct, the white dorsal markings form only rings and not dots, and *C. sykesi* lacks rachidian teeth (ELIOT, 1904:388).

Chromodoris briqua Marcus & Burch, 1965, is also similar in color, but has no white markings on the dorsum. Most significantly, it has a strongly developed rachidian tooth with a pronounced cusp (MARCUS & BURCH, 1965: 246–247, fig. 22).

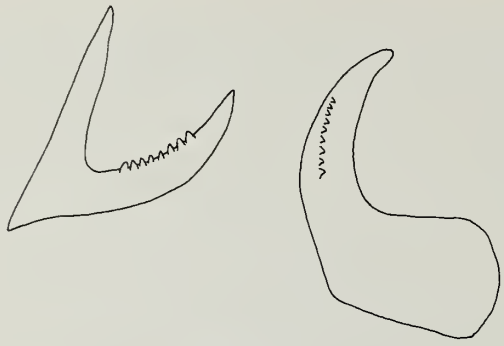

Figure 19

Line drawings of radular teeth of *Glossodoris* ***poliahu*** sp. nov.

Glossodoris Ehrenberg, 1831

Glossodoris ***poliahu*** Bertsch & Gosliner, sp. nov.

(Figures 4, 19–25)

References:
Snowflake: Bertsch & Johnson, 1980:73–77; Bertsch & Johnson, 1981:59 (color photograph).

Material examined: (1) Holotype, CASIZ 064810; collected subtidally, 17 m, off the Lanai Lookout, Oahu, 26 September 1978; HB (*ex* HB 730).

(2) 3 paratypes, CASIZ 064811; collected subtidally at Pupukea, Oahu, 26 May 1978; SJ (*ex* HB 607).

(3) 1 dissected paratype, CASIZ 066611; collected subtidally at Pupukea, Oahu, 26 May 1978; SJ.

(4) Paratype, CASIZ 064812; collected subtidally, 10 m, off Makua, Oahu, 14 September 1987; TMG.

(5) 4 paratypes, LACM 2295; collected at night, subtidally, 15 m, Pupukea, Oahu, 12 June 1978; SJ (*ex* HB 617).

(6) 4 paratypes, LACM 2296; collected subtidally, 15 m, Three Tables, Oahu, 10 June 1978; SJ (*ex* HB 622).

Distribution: Specimens are known from sites on the island of Oahu (also including Yokohama, Ewa, and Koko Head), and from Puako on the island of Hawaii (approximately 19°49′N, 155°47′W). Most animals occurred in water 9–15 m deep.

Etymology: While collecting this unnamed animal, we provisionally called it "snowflake," calling attention to the white frosting specks on its dorsum. Hence it is appropriate to name the species ***poliahu,*** after the Hawaiian goddess of the snow-covered mountain. According to legend, the snow goddess Poliahu lives on the snowy summit of Mauna Kea. While the goddess Pele pours fiery lava over the land from the volcano Mauna Loa on the south side of Hawaii, at the other end of the island Poliahu spreads her cooling mantle of snow (Beckwith, 1970).

(For euphony, we treat the species-group name as a noun in apposition. Although we are aware of ICZN recommendation 31A, against such use, our adding adjectival or genitival suffixes would have resulted in an unnecessarily complicated word to pronounce; four syllables is enough.)

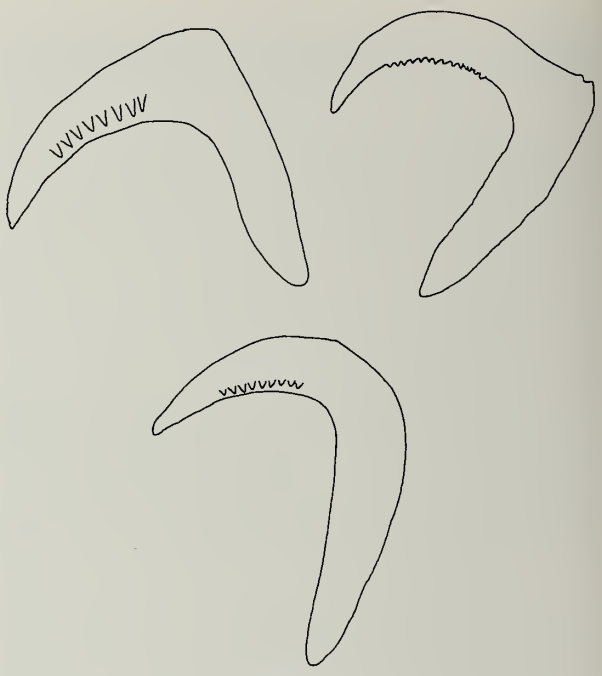

Figure 20

Line drawings of radular teeth of *Glossodoris* ***poliahu*** sp. nov.

External morphology: Preserved specimens measured between 15 and 25 mm total length; living animals are usually between 25 and 35 mm long.

The animals are an elongate ovoid, low in profile, with the foot protruding slightly beyond the posterior portion of the mantle (Figure 4). The mantle overhangs the sides of the body, and is usually convoluted; however, the animal is not as "elevated" as is typical for species of *Glossodoris,* and the mantle margin is much broader with a greater overhang (*cf.* Rudman, 1984). The rhinophores are about evenly spaced from the edges of the body and from each other. They are dusty cream colored, with a light rust-brown vertical streak on both the anterior and posterior surfaces, which bifurcates basally on the posterior side.

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Explanation of Figures 21 to 24

Figures 21–24. Scanning electron micrographs of radula and jaws of *Glossodoris* ***poliahu*** sp. nov. Illustrated specimen is CASIZ 066611.

Figure 21. Rachidian and inner lateral teeth.

Figure 22. Radular teeth from middle of half-row.

Figure 23. Outer lateral teeth.

Figure 24. Jaw armature of bifid rods.

21
060915 15KV Xi.30K 23.1um

22
060916 15KV Xi.20K 25.0um

23
060917 15KV Xi.10K 27um

24
060914 15KV Xi.97K 15.8um

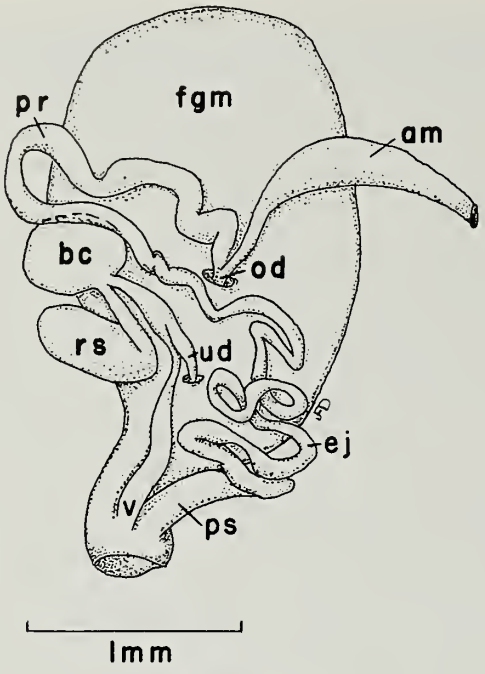

Figure 25

Reproductive system of *Glossodoris* ***poliahu*** sp. nov. Illustrated specimen is CASIZ 066611. Lettering symbols as in Figure 12. Scale = 1 mm.

The 10–14 gills are spread out widely, with 5 or 6 pinnae coming off each side of a lateral, central axis. They are arranged in the characteristic double spiral of *Glossodoris*. The gills are dusky cream, lined along the longitudinal axis (from which extend the pinnae) with a light rust brown coloration.

The dorsum is a light brown color, with white dots sprinkled densely throughout the entire brownish area. The mantle margin has a white band. The extreme edge has a narrow light golden brown line totally encircling it. Another line of the same color occurs in the same location on the ventral side of the mantle margin. Between these two colored lines (on the very edge of the frilly mantle margin) is a thin white line. The upper surface of the foot is encircled marginally by a similar broad white band and narrow light golden brown line.

Buccal mass and radula: The buccal apparatus consists of a large muscular buccal mass and an elongate, glandular oral tube.

The radular formula of the specimen collected 26 September 1978 is 64 × 49·1·49. The rachidian is a small, narrow, elongate plate. The innermost lateral teeth have 3 or 4 denticles on both the inner and outer surfaces of the erect cusp (Figure 21) (for terminology of radular teeth, *cf.* BERTSCH, 1977). The next few inner laterals have denticles on the outer side, which become posteriorly placed as the erect cusp elongates at about the fourth or fifth lateral tooth. Each tooth from the center of a half-row has a long recurving cusp with 6–9 posterolateral denticles (Figures 19, 20, 22). Outermost lateral teeth become shorter, losing pronounced denticulation (Figure 23). The jaw elements are bifid (Figure 24).

Reproductive system: The reproductive system is triaulic (Figure 25). The ampulla is short, widest in the middle. It bifurcates into a short oviduct and a highly convoluted vas deferens. The proximal portion of the vas deferens is prostatic, while the more distal portion is thin, more highly convoluted and muscular, forming an ejaculatory segment. The distal end of the vas deferens enters the simple penial sac. The uterine duct is elongate and straight. It enters the vagina immediately distal to the junction of the thin-walled, spherical bursa copulatrix and the recurved receptaculum seminis.

Natural history: BERTSCH & JOHNSON (1980) report this subtidal species as most abundant between 9 and 16 m depth at the Lookouts, Pupukea, and Makua (on the island of Oahu).

Discussion: We had difficulty placing this species within a genus. Externally, it appears to be a species of *Glossodoris,* with a convoluted mantle margin and gills arranged in a double spiral. The relatively broad radula bears few radular rows (64) making it similar to the radulae of members of the genus *Chromodoris*. The shape of the radular teeth is somewhat intermediate between *Glossodoris* and *Chromodoris*. The morphology of the reproductive system more closely approaches that of a *Glossodoris,* with an elongate vaginal duct and long, cylindrical prostate (RUDMAN, 1984). *Glossodoris* ***poliahu*** most closely resembles *G. carlsoni* Rudman, 1986a. In *G. carlsoni* there are relatively few radular rows (55) (RUDMAN, 1986a). The two species are similar in their coloration, with pink or orange ground color with white spots, a golden marginal band, and a red vertical stripe on the rhinophores. However, there are consistent external and internal morphological differences between the two species. In *G.* ***poliahu*** the white spots are smaller and more numerous. The red vertical posterior line on the rhinophores bifurcates basally and there are actually two golden marginal bands, one on the dorsal surface of the margin and one ventrally. The jaw elements have more regular, bifurcate apices in *G.* ***poliahu*** than in *G. carlsoni*. In *G.* ***poliahu*** there is a distinct rachidian tooth that is absent in *G. carlsoni*. The innermost lateral teeth of *G.* ***poliahu*** bear denticles on both the inner and outer sides of the central cusp, whereas in *G. carlsoni* denticles are present only on the outer side of the central cusp.

A similar appearing sympatric species is *Glossodoris rufomarginata* (Bergh, 1890), immediately distinguishable by its typical *Glossodoris* radula (RUDMAN, 1986a:144–148), golden brown edge of mantle (without the thin white edge between the golden brown mantle margin line that is characteristic of *G.* ***poliahu***), and whitish dorsum covered with bright golden brown speckles (opposite to the golden brown with minute white spotting of *G.* ***poliahu***); contrast the

color photographs of *G. rufomarginata,* identified as *Chromolaichma youngbleuthi* (Kay & Young, 1969), in Bertsch & Johnson, 1981:59, 68–71.

The seemingly nondescript coloration of *Glossodoris* ***poliahu*** is actually quite distinctive and unique among known species of chromodorids.

Glossodoris ***tomsmithi*** Bertsch & Gosliner, sp. nov.

(Figures 5, 26–30)

References and synonymy:

Chromodoris albonotata (*non* Bergh, 1875): Bertsch & Johnson, 1981:52–53 (color photographs).

Material examined: (1) Holotype, CASIZ 066612; collected subtidally, 13.7 m, Makua, Oahu, 14 September 1978, HB and SJ (*ex* HB 699).

(2) 2 dissected paratypes, CASIZ 064817; collected subtidally, 10 m, Pupukea, Oahu, 11 September 1987; TG.

(3) 1 paratype, CASIZ 064818; collected subtidally, 5 m, Makua, Oahu, 14 September 1987; TG.

(4) 3 paratypes, LACM 2297; collected subtidally, 21 m, off Makaha, Oahu, 17 September 1978; HB and Judith Young (*ex* HB 712).

(5) 1 paratype, LACM 2326; collected subtidally, 15 m, off Blowhole (near Lanai Lookout), Oahu, 26 September 1978; HB and SJ (*ex* HB 729).

Distribution: Specimens are known from subtidal locations in the Hawaiian Islands, on Oahu (from 4.5 to 21 m depth, also including Three Tables, just west of Pupukea) and on Hawaii (along the Kona coast, from 3 to 30 m); and in the Marshall Islands, from Enewetak (Cement Ship Pinnacle and R-Buoy Pinnacle, 6–10 m; approximately 11°20′N, 162°20′E) and Kwajalein (oceanside of Enubuj-Ennylabagan reef, 20 m; approximately 8°46′N, 167°38′E).

Etymology: This species is named for Mr. Tom Smith, of San Diego, California, who has accompanied the senior author on numerous nudibranch research expeditions to Hawaii, Mexico, and California. His skills at spotting nudibranchs are matched by his diving abilities and his generosity in supplying equipment when items are not brought to the dive site.

External morphology: The elongate animal has a convoluted overhanging notal margin, with the posterior portion of the foot protruding beyond (Figure 5). The rhinophores and gills are set at approximately one-fifth and four-fifths, respectively, the distance between the anterior and posterior edges of the notum. The rhinophores (17 or 18 perfoliations) are white basally; the distal two-thirds are dark brown (some a dark golden-brown or brass color, others nearly a dark steel color), with a prominent vertical opaque white line on the anterior and posterior faces. The 8–11 branchial plumes are arranged in a double spiral (the attachment points of the posterior smaller plumes curl slightly inward, scroll-like); the central stalks are whitish, fading to a dark steel or blue black along the pinnae. Some animals had this dark blue coloration tinting the basal portions of the interior of the gill circlet.

The dorsum and sides of the foot are a dirty cream white, with a yellow marginal band on the foot. The dorsum is spotted with circular, 1–2-mm-diameter white dots that vary in number, size, and placement. The body is also rimmed by a white marginal band; the extreme edge of the overhanging margin has a very thin bright yellow tint.

The Hawaiian and Marshall Islands specimens differ slightly in coloration. Mr. Scott Johnson has generously provided us with the following description of specimens from Enewetak and Kwajelein:

"The mantle is soft, elongate oval, rounded anteriorly, and slightly more pointed posteriorly. The margin is relatively thick and wide, and is highly undulate. The base mantle color is gray brown, more brown over the gut, and minutely speckled with dark brown or dark gray black. The mantle is margined by a wide yellowish white band. The brownish dorsum is spotted with slightly pustulose yellowish white spots measuring one to two millimeters in diameter (in a 22-mm specimen). The spots tend to be most crowded around the rhinophores and gills, often leaving a blank spot in the middle of the dorsum. The sides of the body are light brownish, minutely speckled with black and crowded with slightly raised yellowish white spots similar to those on the dorsum. The foot is margined by a yellowish white band, and the oral tentacles are creamy yellowish and relatively long. The tail is fairly short and rounded at the end. The rhinophores are relatively tall and pointed, and extend from slightly elevated sheaths. Peduncles are transparent anteriorly and white posteriorly. Rhinophore clubs are brown, finely speckled with black, giving them a gray brown appearance. The clubs each have white anterior and posterior vertical lines and 18–20 lamellae. Branchiae consist of about eight vibratile, quadrangular stalks bearing lamellate pinnae and arranged in an incomplete circle around the anus. The stalks are bluish white, becoming more bluish toward the tips, and the pinnae are edged with black."

The differences can be summarized as follows: the Hawaiian specimens have an overall lighter colored mantle, whiter dorsal spots, darker rhinophore clubs and gill stalks, and a thin yellow marginal edge to the overhanging notum with a wide submarginal white band.

Buccal mass and radula: The buccal apparatus consists of a large muscular buccal mass and an equally elongate, glandular oral tube.

The jaws are densely covered with numerous rodlets. Each rodlet has a simple or, more commonly, bifid cusp (Figure 26). The radular formula in one specimen was 53 × 36·1·36. The rachidian tooth (Figure 27) is a vestigial linear ridge. The innermost lateral teeth have 3 or 4 denticles inside the triangular central cusp and 4 or 5 denticles

26
092927 15KV X3.50K 8.6um

27
101931 15KV X1.70K 17.6um

28
092926 15KV X1.70K 17.6um

29
092925 15KV X1.30K 23.1um

on the outer side. Lateral teeth from the middle of the radular half-row are curved and elongate with 6–8 denticles below the central cusp (Figure 28). The outermost laterals bear 6–12 denticles below the central cusp (Figure 29). The radular formulae of two specimens from Enewetak were 62–73 rows, with 42–56 teeth per half-row.

Reproductive system: The reproductive system (Figure 30) is triaulic. The preampullary duct is narrow and expands into the saccate ampulla. At its distal end, the ampulla narrows and divides into the short oviduct and elongate vas deferens. The proximal portion of the vas deferens is narrow, highly convoluted, and prostatic. More distally, it becomes more muscular and widens in the ejaculatory portion. The penis is simple. The uterine duct is short and straight. The bursa copulatrix is thin walled and spherical. The receptaculum seminis is pyriform and recurved. The vagina is thin and elongate. The uterine duct branches from the distal third of the vagina and enters the female gland mass after a short distance.

Discussion: Like the preceding species, *Glossodoris* ***tomsmithi*** has features somewhat intermediate between *Glossodoris* and *Chromodoris*. Its convoluted mantle margin, vibratile gills arranged in a double spiral, elongate vaginal duct, and long, cylindrical prostate are characteristic of *Glossodoris*. However, the shape of the radula and relatively low number of radular rows (53–73) are similar to *Chromodoris*.

Glossodoris ***tomsmithi*** is similar to *G. carlsoni* and *G.* ***poliahu*** in its body shape and radular morphology. It differs markedly in its coloration from both other species. *Glossodoris* ***tomsmithi*** has a vestigial rachidian tooth, whereas *G.* ***poliahu*** has a prominent rachidian and *G. carlsoni* entirely lacks a rachidian.

This Hawaiian species had been considered conspecific with the Tahitian *Chromodoris albonotata* Bergh, 1875. However, there are a number of critical differences in the body shape, gills, coloration (noted by RUDMAN, 1986a: 166), and radular morphology that distinguish this new species from Bergh's. In specimens of approximately equal size, *C. albonotata* was reported to have six branchial plumes arranged in a simple circle (BERGH's [1875] illustration shows them thin, elongate, and sparse) and 30 rhinophoral perfoliations (BERGH, 1879:5–6). By contrast, *G.* ***tomsmithi*** has 8–11 branchial plumes arranged in a double spiral, and 17 or 18 perfoliations on the rhinophore. The

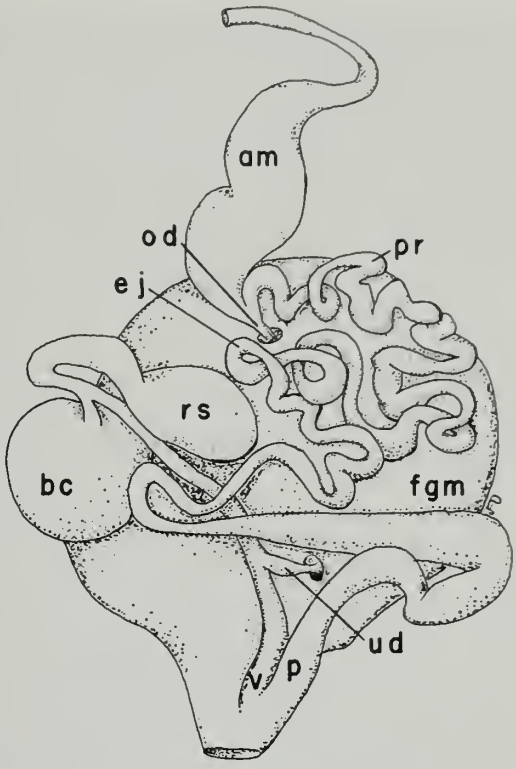

Figure 30

Reproductive system of *Glossodoris* ***tomsmithi*** sp. nov. Illustrated specimen is CASIZ 064817. Lettering symbols as in Figure 12. Scale = 1 mm.

mantle margin of *C. albonotata* is smooth, whereas that of *G.* ***tomsmithi*** is convoluted. The basic dorsal color of *C. albonotata* is yellowish (BERGH, 1875:pl. VII), but that of *G.* ***tomsmithi*** is dirty white. *Chromodoris albonotata* lacks dark pigment on the gills and rhinophores. The radula is especially different: *C. albonotata* has a smaller number of rows of teeth (38) than teeth per half-row (45). This relation is reversed in *G.* ***tomsmithi***: 53 rows, 36 teeth; 62 rows, 42 teeth; and 73 rows, 56 teeth (see BERTSCH, 1976, for a discussion of statistical analyses of radular variation).

Ardeadoris Rudman, 1984

Ardeadoris ***scottjohnsoni*** Bertsch & Gosliner, sp. nov.

(Figures 6, 31–35)

References and synonymy:
Chromodoris sibogae (*non* Bergh, 1905): BERTSCH & JOHNSON, 1981:49 (color photographs).

Material examined: (1) Holotype (dissected), CASIZ 064813; collected subtidally, 5 m, Kahe Point, Oahu, July 1973; TG.

←

Explanation of Figures 26 to 29

Figures 26–29. Scanning electron micrographs of radula and jaws of *Glossodoris* ***tomsmithi*** sp. nov. Illustrated specimen is CASIZ 064817.

Figure 26. Bifid jaw rodlets.

Figure 27. Rachis area of radula.

Figure 28. Lateral teeth from middle of half-row.

Figure 29. Outer lateral teeth.

31
092904 15KV X3.00K 10.0um

32
101934 15KV X1.20K 25.0um

33
101936 15KV X1.30K 23.1um

34
092903 15KV X1.69K 18.8um

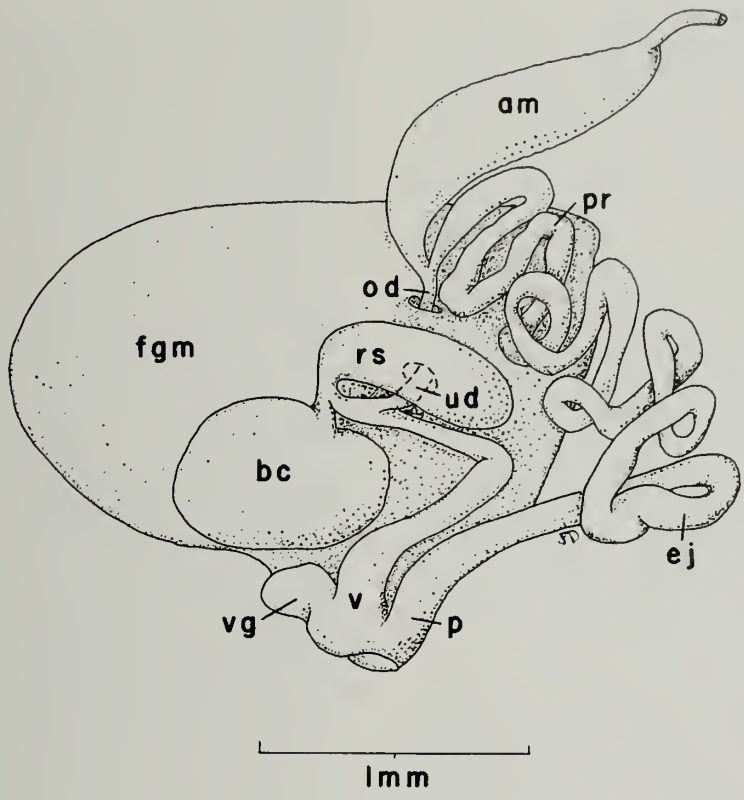

Figure 35

Reproductive system of *Ardeadoris* ***scottjohnsoni*** sp. nov. Illustrated specimen is CASIZ 064813. Lettering symbols as in Figure 12. Scale = 1 mm.

(2) 1 dissected paratype, CASIZ 064814; collected subtidally, 15 m, Pupukea, Oahu, 15 August 1978; SJ.

Distribution: We have records of *Ardeadoris* ***scottjohnsoni*** also occurring at Yokohama on Oahu, and at Puako on Hawaii. It is presently known from subtidal locations on two of the Hawaiian Islands (Oahu and Hawaii).

Etymology: This species is named in honor of our good friend and colleague Mr. Scott Johnson, in recognition of his many contributions to our understanding of the taxonomy and biology of Indo-Pacific nudibranchs. We especially thank him for a generous scientific attitude and his willingness to share specimens he has collected, his field knowledge, and his superb photographs of the living organisms.

External morphology: Living animals are about 15–25 mm long. The body shape is elongate, with the posterior portion of the foot protruding slightly past the hind margin of the animal's notum (Figure 6). The overhanging notal margin has slight notchlike crenulations, with a more prominent wavy crenulation about midway down the length of the body. The 10 simply pinnate gills are white basally, with the distal two-thirds black. The animal vibrates the gills (which are usually held partly upright, slightly spread). The rhinophores are black with a thin vertical white line on the anterior face.

The dorsum and sides of the foot are pure white; both regions are encircled by an even whiter marginal band. Surrounding the white notal band is a thin yellow orange stripe at the edge of the overhanging margin.

Buccal mass and radula: The buccal apparatus consists of an elongate, muscular buccal mass and a large, glandular oral tube.

The jaws are thin and covered with simple or bifid

←

Explanation of Figures 31 to 34

Figures 31–34. Scanning electron micrographs of the jaw and radula of *Ardeadoris* ***scottjohnsoni*** sp. nov.

Figure 31. Jaw with simple rodlets. Illustrated specimen is CASIZ 064814.

Figure 32. Rachidian and central region of radula, showing innermost lateral teeth in the half-row. Illustrated specimen is CASIZ 064813.

Figure 33. Inner- and mid-lateral teeth. Illustrated specimen is CASIZ 064813.

Figure 34. Lateral teeth from central portion of half-row. Illustrated specimen is CASIZ 064814.

conical rodlets (Figure 31). The radular formula of the single specimen examined was 42 × 15·1·1·1·15. There is a faint trace of a rachidian row of teeth (Figures 32, 33). The inner lateral teeth (Figures 32, 33) are elongate and sickle-shaped, with 5–8 rounded denticles on the inner margin of the teeth. The succeeding lateral teeth are curved, elongate, with 3–6 palmately divided denticles on their distal tip (Figure 34).

Reproductive system: The arrangement of organs (Figure 35) is triaulic. The narrow preampullary duct expands into a short, saccate ampulla. The ampulla narrows distally, and bifurcates into the short oviduct and vas deferens. The vas deferens is highly convoluted. In its proximal portion it is prostatic and becomes muscular in the most distal ejaculatory segment. The penial sac is relatively short and bulbous. The spherical bursa copulatrix and the recurved, pyriform receptaculum seminis are adjacent to each other. Immediately distal to the insertion of the bursa and receptaculum onto the vagina is the branch of the uterine duct to the female gland mass. The vagina is elongate and curved. A small spherical vestibular gland appears to be present at the base of the vagina.

Discussion: This species is difficult to place definitely within a genus. It bears similarities to members of the genera *Thorunna* Bergh, 1877b, and *Ardeadoris* Rudman, 1984. Rudman (1984) discussed the similarity of the two genera and distinguished *Ardeadoris* (based solely on the single species *A. egretta* Rudman, 1984) by its convoluted, overhanging mantle edge, rather than a slightly undulating edge in *Thorunna.* In *A. **scottjohnsoni*** the mantle is less convoluted than in *A. egretta,* but more pronounced than in most species of *Thorunna.* In *Ardeadoris egretta* the radula is fairly broad, whereas in *A. **scottjohnsoni*** and species of *Thorunna* it is much narrower, with fewer teeth per row. *Ardeadoris* has multifid outer lateral teeth as in *A. **scottjohnsoni,*** whereas species of *Thorunna* have bifid outer laterals. The inner lateral teeth of *A. **scottjohnsoni*** are similar in shape to both *A. egretta* and *Thorunna furtiva* Bergh, 1878 (Rudman, 1984:figs. 33c, 76a). In both species of *Ardeadoris* the reproductive system contains a simple vestibular gland and the uterine duct branches at the bases of the receptaculum seminis and bursa copulatrix. In all species of *Thorunna* that have been studied the vestibular gland is more complex and usually highly ramified and the uterine duct branches from near the middle of the vagina. In the future, it is likely that the systematic status of the genus *Ardeadoris,* or *A. **scottjohnsoni*** in particular, may need to be re-evaluated. For the present, we believe that *A. **scottjohnsoni*** is better placed in *Ardeadoris* rather than *Thorunna.*

*Ardeadoris **scottjohnsoni*** is the only species of *Ardeadoris* or *Thorunna* with black pigment on the gills and rhinophores.

This species superficially resembles the description of *Chromodoris sibogae*: "Die Farbe war durchgehends weisslich, vorne und hinten am Rücken so wie an den Körperseiten schmutzig gelblich; oben am Rückengebräme, dessen Rand eine graue sehr ausgeprägte Linie zeigte, kamen sparsam zerstreute, runde und mehr unregelmässige, kalkweisse Flecke . . .; die Keule der Rhinophorien so wie die Kiemenblätter braungrau" (Bergh, 1905:157). Bergh's description appears to be of a preserved specimen; however, the recent rediscovery of this species (and transferral to the genus *Glossodoris*) by Rudman (1986a:112–116) indicates that color differences are not preservation artifacts but specific characteristics. *Glossodoris sibogae* is brownish-yellow, with a submarginal white band and an outer black border. *Ardeadoris **scottjohnsoni*** has a distinctly white body and an outer yellow-orange band surrounding the white submarginal band. Moreover, the elongate glossodorid radula with simply cusped teeth (the inner teeth usually bear accessory lateral denticles) is immediately distinguished from the ardeadorid radula with the palmately divided apices of the individual teeth. Rudman (1986a) has also shown that *G. undulata* Pruvot-Fol, 1954, is a junior synonym of *G. sibogae*; and he has detailed the characteristics that separate *G. sibogae* from *G. atromarginata* (Cuvier, 1804), both of which have a marginal black band (not yellow orange as in *A. **scottjohnsoni***). The specimens reported by Eliot (1913) and Baba (1949) as *G. sibogae,* from Japan, represent the recently described species *Glossodoris misakinosibogae* Baba, 1988.

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Successful and Unsuccessful Drilling Predation in Recent Pelecypods

by

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Abstract. A survey of 43 samples of empty Recent pelecypod valves from seven cold-temperate and 10 tropical shallow-water sites revealed an equatorward decrease in the incidence of complete gastropod drill holes. This result, which runs counter to earlier studies of drilling in turritellid gastropods, is consistent with the generalization that slow methods of predation (including drilling) decrease in importance toward the tropics because they place the predators at undue risk. Among naticid-drilled pelecypods, there is also an equatorward decrease in the incidence of incomplete drill holes.

Analysis of a sample of *Pseudocardium sachalinense* (Schrenck, 1862) from Hokkaido, Japan, suggests that incomplete holes usually represent unsuccessful drilling attacks. Because complete and incomplete holes in this sample were statistically indistinguishable with respect to both size and position, we were unable to identify specific shell features contributing to the high overall effectiveness of the shell of *P. sachalinense* as protection against drilling by naticids.

INTRODUCTION

Drilling is a common form of predation on shell-bearing marine invertebrates. Using chemical and mechanical means, the predator (usually a gastropod or octopod) excavates a hole through the prey's shell wall. In most cases, a hole that completely penetrates through the shell indicates successful predation, whereas an incomplete drill hole, which does not reach the inner shell surface, generally indicates unsuccessful drilling. Although exceptions occur (see below), the distinction between complete and incomplete drill holes in a sample of "dead" shells makes it possible to infer predation success during the subjugation phase of a drilling predator's attack. This, in turn, makes drilling ideal for the study of geographical and temporal patterns in predation intensity.

Previous studies have generally pointed to the conclusion that drilling is ecologically and evolutionarily more important in the tropics than at higher latitudes. Tropical turritellid gastropods show higher frequencies of complete drill holes among empty shells than do temperate species (DUDLEY & VERMEIJ, 1978; ALLMON *et al.*, 1989). This pattern parallels the equatorward increase in the diversity of drilling gastropods (MARINCOVICH, 1977; TAYLOR & TAYLOR, 1977). A latitudinal pattern in the distribution of incomplete drill holes, and therefore in the effectiveness of shell armor as a defense against drilling, might also be expected, because the expression of shell armor among mollusks generally increases from high to low latitudes (VERMEIJ, 1978, 1987). No evidence on this expectation has been published to date. However, most mobile mollusks seem to have adapted against drilling predators not through the development of thick armor, but by emphasizing attributes enabling the prey to avoid detection or to escape before being caught (VERMEIJ, 1978, 1987). Not only do many species show well-developed escape responses to drilling gastropods, but most drilling attempts by naticacean gastropods appear to be successful, judging from the low frequencies of incomplete holes in most prey species. High frequencies of incomplete holes (and therefore presumably of unsuccessful attacks during the subjugation phase) are reported mainly for the sedentary prey of muricacean drillers (ADEGOKE & TEVESZ, 1974; KOJUMDJIEVA, 1974; BLACK, 1978; VERMEIJ, 1980b, 1987; PALMER, 1982). If muricaceans fail more often than do naticaceans in attempting to drill their prey, an equatorward increase in drilling-related armor might occur only among the prey of muricaceans.

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The evaluation of these ideas requires the analysis of systematically collected samples of empty shells from many geographical localities. In this paper, we report the results of surveys conducted by us during the last 12 yr on frequencies of complete and incomplete drilling in shallow-water pelecypods from various temperate and tropical localities. As will be seen, most of the generalizations that have been made about drilling are challenged by the new evidence.

MATERIALS AND METHODS

The localities at which we surveyed empty pelecypod valves are listed in Table 1. At each site, all intact paired and unpaired valves were collected from the beach surface. We assumed that valve sorting by waves and shell collecting by beach-goers did not materially alter the incidence of complete and incomplete drill holes in the population. That these assumptions are valid is suggested by the fact that the observed frequencies of complete and incomplete drilling in paired valves were statistically indistinguishable from the respective frequencies in unpaired valves in all samples. Each shell in a sample was carefully scanned for the presence of complete and incomplete drill holes. Samples of all species are conserved in the Vermeij collection; a subsample of *Pseudocardium sachalinense* from Locality 2 has been deposited at the U.S. National Museum of Natural History in Washington.

The incidence of complete and incomplete drilling was calculated as the number of holes divided by the number of individuals. The number of individuals was taken as the number of valve pairs plus half the number of unpaired valves. Drilling was assessed only in intact valves. This restriction may lead to an overestimation of the importance of drilling as a cause of mortality because individuals dying as a result of shell breakage are excluded (VERMEIJ, 1980a), but it should not affect the calculation of drilling success (the number of incomplete drill holes divided by the total number of holes). The incidence of complete holes was assessed only in samples of 10 or more individuals; drilling success was calculated only in samples in which the total number of drill holes was 10 or more.

In order to determine whether and how complete drill holes differ from incomplete ones, we measured the outer diameter of each hole (that is, the diameter as seen on the shell's exterior) and calculated the position of each hole along the anteroposterior and dorsoventral axes of the valve. The anteroposterior position was calculated as the distance from the anterior edge of the shell to the anterior edge of the hole divided by the anteroposterior length of the shell along a line passing through the middle of the hole. Similarly, the dorsoventral position of the hole was calculated as the distance from the dorsal edge of the valve to the dorsal edge of the hole divided by the dorsoventral length of the shell along a line passing through the middle of the hole.

The identity of drilling predators was inferred from the shapes of drill holes (see CARRIKER & YOCHELSON, 1968), from direct observations of predation, and from the co-occurrence of known drillers. Muricacean holes are nearly cylindrical and have an evenly rounded bottom if incomplete, whereas naticacean holes (Figure 1) are markedly tapered and have a slightly raised bottom when incomplete.

Table 1

Localities of samples of empty pelecypod valves.

Locality 1. Abashiri City, moderately exposed sand beach on Okhotsk Sea, north coast of Hokkaido, Japan, taken 14–16 July 1988, by G.J.V., E.C.D., and E.Z. Likely predator: *Natica* (*Tectonatica*) *janthostoma* (Deshayes, 1841).

Locality 2. Tsukushikoi, exposed sand beach at Cape Aikappu, southeastern Hokkaido, Japan, taken 21–31 July 1988, by G.J.V., E.C.D., and E.Z. Likely predator: *N. janthostoma*.

Locality 3. Akkeshi Bay, sheltered shore of cobble and sandy silt at Akkeshi Marine Biological Station, southeastern Hokkaido, Japan, taken 31 July and 1 August 1988, by G.J.V., E.C.D., and E.Z. Likely predators: *Ocenebra japonica* (Dunker, 1860) and *O. adunca* (Sowerby, 1834).

Locality 4. Outer part (Nakanose) of Akkeshi Bay, heavily bioeroded mudstone at depth of 4 m, the pelecypods in abandoned pholad holes, taken 20 July 1988, by G.J.V. and E.C.D. Likely predator: *Nucella freycinetii* (Deshayes, 1841).

Locality 5. Cape Elizabeth, south of Portland, Maine, USA, tidepool at mid-tide level; taken 11 August 1988, by G.J.V. and E.Z. Predator: *Nucella lapillus* (Linnaeus, 1758).

Locality 6. Sheep Island, off Deer Isle, Maine, taken 24 August 1988, by E.C.D. Predator: *N. lapillus*.

Locality 7. Fay Beach, Vineyard Sound, Massachusetts, depth of 1.5 m on sand; taken 10 August 1988, by E.C.D. Likely predator: *Euspira heros* (Say, 1822).

Locality 8. Wom Village, west of Wewak, Papua New Guinea, sheltered sand beach; taken 23–24 June 1979, by G.J.V. and E.Z. Likely predators: various naticids, especially *Polinices* (*P.*) *tumidus* (Swainson, 1840).

Locality 9. Suva Point, Viti Levu, Fiji, mudflat; taken 23 March 1986, by G.J.V. Likely predators: various naticids.

Locality 10. El Playon, Bahia de Amuay, west coast of Paraguana Peninsula, Venezuela, sand beach; taken 13–17 July 1977, by G.J.V. and E.Z. Likely predators: various naticids.

Locality 11. Las Lajas, Pacific coast of Chiriqui Province, Panama, exposed sand beach; taken 17–20 July 1978, by G.J.V. and E.Z. Likely predators: various naticids.

Locality 12. Playa Brava, Pacific coast of Veraguas Province, Panama, relatively sheltered sand beach; taken 21–25 August 1978, by G.J.V. and E.Z. Likely predators: various naticids.

Locality 13. Isla Naos, Pacific coast of Panama Province, Panama, sheltered sand beach; taken 7–26 February 1986, by G.J.V., E.C.D., and E.Z. Likely predators: various naticids.

Locality 14. Playa Vernado, Pacific coast of Panama Province, Panama, sheltered sand beach and mudflats; taken April to June 1976, by G.J.V. and E.Z. Likely predators: various naticids.

Locality 15. Playa Venado; taken July 1978, by G.J.V. and E.Z.

Locality 16. Playa Venado; taken February 1986, by G.J.V., E.C.D., and E.Z.

Locality 17. Punta Chame, Pacific coast of Panama Province, Panama, exposed sand beach; taken 9 February 1986, by G.J.V. and E.C.D. Likely predators: various naticids.

Figure 1

Incomplete drill hole, presumably made by the naticid *Natica janthostoma,* on a valve of *Pseudocardium sachalinense* from Locality 2 (Tsukushikoi, Hokkaido, Japan).

RESULTS AND DISCUSSION

Geographical Patterns in Complete Drilling

Drilling is an important cause of death in many pelecypod species. The survey in Table 2 shows that drilling frequencies exceeding 0.50 occur in 2 of 13 cold-temperate samples (15%) and in only 2 of 30 tropical samples (6.7%). Contrary to the situation in the gastropod family Turritellidae, in which an equatorward increase in drilling frequency was found (DUDLEY & VERMEIJ, 1978; ALLMON *et al.,* 1989), the data on pelecypods point to a poleward increase in drilling. A nonparametric comparison between the 30 tropical samples and the 13 cold-temperate samples of Table 2, together with drilling frequencies of four additional cold-water samples reported by SCHÄFER (1972) from the North Sea and by COMMITO (1982) from Maine, shows that the frequency of complete drilling is significantly lower in the tropics (median frequency 0.09) than in the cold-temperate areas (median frequency 0.24, $P < 0.01$, Mann-Whitney U-test).

Additional data in the literature suggest that our tropical samples were very similar to previously studied material from tropical sites with respect to the distribution of drilling frequencies. The median frequency of complete drilling in these samples from Guam (VERMEIJ, 1980a), Indonesia (VERMEIJ, 1980b), and Barbados (SANDER & LALLI, 1982) is 0.09, a value identical to that in the tropical samples of Table 2.

Only one study of drilling predation has been done in the polar regions. AITKEN & RISK (1988) report drilling frequencies of 0.01 to 0.90 among four Recent shallow-water pelecypod species from Clyde River in the eastern Canadian Arctic. Late Pleistocene and Holocene samples of these and other species at other Arctic sites generally show drilling frequencies below 0.10; only 1 of 15 samples (6.7%) shows a frequency of complete drilling higher than 0.50. These frequencies are thus more like those in the tropics than the cold north temperate zone.

Two small surveys of warm-temperate pelecypod drilling have been published, one on seven species in Italy (VIGNALI & GALLENI, 1986) and one on three species in South Australia (LAWS & LAWS, 1972). Both surveys report high frequencies of drilling (median frequency 0.21) comparable to the high values reported here for cold-temperate samples. Other scattered reports on warm-temperate thin-shelled pelecypods in Japan (MUKAI, 1972), Ireland (NEGUS, 1975), and the eastern United States (FRANZ, 1977; ROSEWATER, 1980; WILTSE, 1980) similarly indicate high frequencies of complete drilling.

Like other forms of predation, drilling varies greatly in its intensity on a small spatial scale as well as over time at individual sites (VERMEIJ, 1980a; WILTSE, 1980; COMMITO, 1982). Geographical patterns must therefore be very strong if they are to be detected above the "noise" of local and short-term temporal variation. The limited data at hand, most of which come from the northern hemisphere, suggest that the highest frequencies of complete drilling occur at mid-latitudes, with lower frequencies being

Table 2

Incidence of complete (C) and incomplete (I) drilling (expressed as percentage of individuals) in empty pelecypod valves.

Species	Lc.	*n*	C	I	Eff.
Mactra (*M.*) *chinensis* (Philippi, 1846)	1	44.5	81%	16%	0.16
Pseudocardium sachalinense (Schrenck, 1862)	1	10.5	38%	9%	—
Peronidia venulosa (Schrenck, 1861)	1	11	45%	9%	—
Pseudocardium sachalinense	2	122	16%	25%	0.61
Peronidia venulosa	2	30.5	16%	33%	0.67
Protothaca (*Callithaca*) *adamsi* (Reeve, 1863)	3	87	26%	8%	0.23
Clinocardium californiense (Deshayes, 1839)	3	11	0	0	—
Clinocardium uchidai Habe, 1955	3	40	0	0	—
Protothaca (*Novathaca*) *euglypta* (Sowerby, 1914)	4	18	94%	6%	0.06
Mytilus edulis Linnaeus, 1758	5	56.5	26%	0	—
Mytilus edulis	6	37	14%	3%	—
Spisula (*Hemimactra*) *solidissima* (Dillwyn, 1817)	7	60	5%	2%	—
Cochlodesma leanum (Conrad, 1831)	7	13	23%	0	—
Meretrix lusoria (Röding, 1798)	8	35	9%	0	—
Codakia (*Ctena*) *bella* (Conrad, 1837)	9	22	9%	0	—
Anadara inaequivalvis (Linnaeus, 1758)	9	14	0	7%	—
Mactra (*Mactrotoma*) *fragilis* (Gmelin, 1791)	10	11.5	0	0	—
Pitar (*P.*) *albida* (Gmelin, 1791)	10	18.5	22%	0	—
Protothaca (*Leukoma*) *granulata* (Gmelin, 1791)	10	20.5	29%	0	—
Chione (*C.*) *cancellata* (Linnaeus, 1767)	10	10	0	0	—
Mactrellona exoleta (Gray, 1847)	11	21.5	9%	2%	—
Tivela (*T.*) *byronensis* (Gray, 1838)	11	26	12%	0	—
Tivela (*Planitivela*) *planulata* (Broderip & Sowerby, 1830)	11	14.5	0	0	—
Pitar (*Hysteroconcha*) *lupanaria* (Lesson, 1830)	11	16.5	36%	0	—
Pitar (*H.*) *brevispinosus* (Sowerby, 1851)	11	12	25%	0	—
Pitar (*Lamelliconcha*) *unicolor* (Sowerby, 1835)	11	14	0	0	—
Donax carinatus Hanley, 1843	11	28	0	0	—
Megapitaria squalida (Sowerby, 1835)	12	11.5	43%	0	—
Protothaca (*Tropithaca*) *grata* (Say, 1831)	13	57	2%	4%	—
Laevicardium (*L.*) *elenense* (Sowerby, 1840)	13	15.5	0	0	—
Donax gracilis Hanley, 1845	13	19.5	13%	0	—
Diplodonta subquadrata (Carpenter, 1856)	13	39.5	17%	0	—
Mactrellona exoleta	14	16.5	16%	0	—
Dosinia dunkeri (Philippi, 1844)	14	19.5	36%	0	—
Tellina (*Eurytellina*) *laceridens* Hanley, 1844	14	23	4%	0	—
Mactrellona exoleta	15	11.5	0	0	—
Tellina laceridens	15	19	5%	0	—
Tellina (*Angulus*) *subtrigona* (Sowerby *in* Reeve, 1866)	15	10.5	0	0	—
Temnoconcha cognata C. B. Adams, 1852	15	28.5	7%	0	—
Tagelus peruvianus Pilsbry & Olsson, 1941	15	12	0	0	—
Chione (*Iliochione*) *subrugosa* (Wood, 1828)	16	29	78%	7%	0.09
Protothaca (*Leukoma*) *mcgintyi* Olsson, 1961	16	10.5	57%	10%	—
Mactrellona exoleta	17	18.5	5%	0	—

Key: Lc.—Locality. *n*—Number of individuals. C—Number of complete drill holes divided by *n*. I—Number of incomplete drill holes divided by *n*. Eff.—Effectiveness of armor: number of incomplete holes divided by total number of drill holes.

more typical of the tropical sites and the one polar area that have been studied to date.

Geographical patterns in drilling may result from systematic variations in the abundance of drilling predators, the abundance or effectiveness of other causes of mortality (especially those that remove shells from the sampled population), or artifacts of taxonomy whereby unusually susceptible groups happen to be well represented in certain geographical regions. We have no data on geographical patterns in the abundance of drilling predators. With respect to the second factor (removal of shells from the sampled population), it may be noted that breakage is a common cause of death in tropical epifaunal and shallow-burrowing pelecypods (Vermeij, 1980a). The frequencies of complete drilling in Table 2 and in Vermeij (1980a) are therefore almost certainly overestimates for the tropical species, because we specifically eliminated broken valves from our survey. The apparent increase in the frequency of complete drilling from the tropics to the northern mid-latitudes may therefore be even greater than our data indicate. Exploitation of clams by humans may also eliminate valves from the population, and would similarly result in

an overestimate of observed frequencies of complete drilling. This is likely to be a problem chiefly in Panama, where several of the sampled species (especially the venerids *Chione subrugosa, Protothaca grata,* and *P. mcgintyi*) are commonly used for food. Although pelecypods are also widely harvested in Japan, the species surveyed by us are apparently not exploited.

Taxonomic artifacts may be investigated by assessing geographical patterns within families. Available data permit the study of only one family, the Mactridae. The six temperate mactrid samples in Table 2 and the literature (Franz, 1977; Vignali & Galleni, 1986), pertaining to the genera *Mactra, Pseudocardium,* and *Spisula,* have significantly higher frequencies of complete drilling ($P < 0.05$) than do the five tropical samples in Table 1 (pertaining to the genera *Mactra* and *Mactrellona,* all from Panama and Venezuela). This pattern therefore conforms with that observed in the entire pelecypod sample.

In a discussion of the various ways in which shell-bearing mollusks are subdued by predators, Vermeij (1987) pointed out that drilling by gastropods is an extremely slow form of predation. Unless drilling is done in habitats where the predator is safe from disturbances by physical agencies or enemies, or unless the predator is itself well adapted to withstand their onslaught, drillers are potentially at great risk while they slowly subdue and consume their prey. Rapid forms of predation, especially shell breakage and shell entry with the aid of anaesthetization or envenomation, are most highly developed among tropical predators, and may be more important causes of death for tropical than for higher-latitude pelecypods (Vermeij, 1978, 1987). The equatorward increase in drilling predation among turritellid gastropods therefore constitutes an odd exception to the rule that slow forms of predation decline in importance toward the tropics. It remains unclear how the turritellid pattern is to be explained. Our results on drilling in pelecypods are at least partly consistent with the idea that slow methods of predation should be more prevalent at higher latitudes.

This interpretation is supported by data on the geographical distribution of two distinct types of drilling in pelecypods, namely, side-drilling and edge-drilling. Side-drilling occurs when the hole passes through the wall of one valve; it is practiced by many muricaceans and most naticaceans (Vermeij, 1978, 1980a; Ansell & Morton, 1987). Edge-drilling occurs when the hole is made at the commissure between the valves; this is done by many muricaceans and some polinicine naticids (Vermeij, 1978, 1980a; Kent, 1981; Ansell & Morton, 1985, 1987). It is likely that edge-drilling is considerably faster than is side-drilling (Ansell & Morton, 1987); hence, it should be more common in the tropics. Our data suggest that this is indeed so. Only 2 of 13 cold-temperate samples (15%) (*Protothaca adamsi* at Locality 3 and *Mytilus edulis* at Locality 6) contained edge-drilled valves, but in both cases edge-drills constituted a minority (11% and 16% respectively) of the total number of complete holes. Among the 30 tropical samples in Table 2, 8 (27%) contained edge-drilled individuals; edge-drills constituted 50% or more of the total number of complete drill holes in *Chione subrugosa* from Locality 16 (100% of holes), *Protothaca mcgintyi* at Locality 16 (50%), and *Pitar albida* at Locality 10 (50%). An earlier survey in Guam also revealed high incidences of edge-drilling among pelecypods on that tropical island (Vermeij, 1980a).

Distribution and Interpretation of Incomplete Drilling

Although incomplete drilling is generally rare in the pelecypods we surveyed (Table 2), it is surprisingly common in the naticacean-drilled species from northern Japan. Indeed, contrary to expectation, our limited data failed to uncover significant differences with respect to the frequency of incomplete drilling in cold-temperate pelecypods between naticacean-drilled and muricacean-drilled samples ($P > 0.10$). Among naticacean-drilled pelecypods, the 20 tropical samples in Table 2 show significantly lower frequencies of incomplete drilling than do the seven cold-temperate ones ($P < 0.02$). This result is strengthened by the observation that none of the naticacean-drilled pelecypods in the samples of dead shells studied by Vermeij (1980a) from Guam contained incomplete drill holes.

Incomplete drill holes have usually been interpreted as unsuccessful predation attempts, but Ansell & Morton (1987) have shown in laboratory trials with *Venerupis japonica* eaten by various naticids that some incompletely drilled prey had nevertheless been consumed by the predator. In such cases, the prey was apparently suffocated while enveloped in the predator's foot, enabling the predator to consume the clam by way of the gape between the valves even before drilling was completed. If such cases are common, instances of successful and unsuccessful drilling cannot be distinguished consistently, so that inferences about the efficacy of drilling predators in fossil assemblages would be tenuous at best.

Analysis of the pattern of occurrence of incomplete drill holes in the sample of *Pseudocardium sachalinense* from Locality 2 suggests strongly that the incomplete holes do indeed represent unsuccessful drilling attacks. We found eight pairs and unpaired valves in which two or more holes had been drilled. In two of these, one of the holes was complete and therefore presumably lethal, whereas the others were incomplete and therefore not lethal. In the other six individuals, all holes (up to four in one pair) were incomplete. Even if one incomplete hole per individual had been lethal, 13 incomplete holes out of a total of 31 incomplete holes in the eight individuals could not have been fatal. Thus, at least 42% of the incomplete holes represent cases of unsuccessful predation. This is certainly an underestimate, because many unpaired valves with incomplete holes may originally have been joined to drilled valves that were not represented in our sample.

Besides the fact that our findings pertain to predators

Table 3

Distribution of drill holes according to shell size in *Pseudocardium sachalinense* from Locality 2 in Hokkaido.

Size class (mm)	*n*	C	I
20–54	21	0.33	0.14
55–64	33	0.27	0.48
65–74	44	0.07	0.09
75–84	74	0.02	0.07
85–94	37	0.05	0.08
95–104	23	0	0
105–119	18	0	0

Key: *n*—Number of valves. C—Frequency of complete drill holes. I—Frequency of incomplete drill holes.

Table 4

Analysis of complete and incomplete drill holes in *Pseudocardium sachalinense* from Locality 2 in Hokkaido.

Characteristic	Complete	Incomplete
Number	18	33
Dorsoventral position on shell	0.44 ± 0.11	0.43 ± 0.12
Anteroposterior position on shell	0.45 ± 0.06	0.48 ± 0.09
Outer diameter	5.74 ± 1.25 mm	5.59 ± 0.82 mm

and prey different from those studied by ANSELL & MORTON (1987), the studies also differ in that ours was based on collections of empty valves from the field, whereas Ansell & Morton's was carried out in the laboratory. In the latter setting, predators can attack prey without risk, and the chance that a given attack can be completed without interruption is high. Just how important such a laboratory artifact is cannot be ascertained at present. Future work comparing laboratory success rates and handling times of predators with field observations on the same species of predator and prey should help to clarify this issue.

Complete as well as incomplete holes were most frequent in the smaller valves of *Pseudocardium sachalinense* (Table 3). The peak frequency of incomplete holes was in the 55–64-mm size class, whereas that of complete holes was in the smallest size class (20–54 mm). This result cannot be taken to imply, however, that unsuccessful drilling is linked with larger prey size than is successful drilling. Individuals that were drilled incompletely were, at least in some cases, able to grow after the attack, whereas completely drilled individuals were not.

It is noteworthy that no shell of *Pseudocardium sachalinense* longer than 93 mm was marked by any drill hole. This observation suggests that clams surviving to the largest sizes were never attacked by naticids and, more interestingly, that individuals with incomplete drill holes (that is, individuals that survived attacks by naticids) did not attain large body sizes. It is therefore possible that unsuccessfully drilled individuals are weakened by the drilling ordeal, making them more susceptible to mortality than are individuals that are never attacked. Indeed, if unsuccessfully drilled individuals commonly grew well beyond the size at which they were attacked, the range of positions of incomplete holes should be considerably greater than the range of positions of complete holes, owing to the fact that the position of the hole changes as the shell of the survivor continues to grow. No such difference was found (Table 4). An alternative interpretation of the absence of large drilled individuals is that the cohort of clams represented in our sample by large adults grew to maturity at a time when naticid densities were low, whereas the cohort represented by smaller individuals lived with a denser predator population. We cannot distinguish between these alternative explanations with presently available evidence.

Because the number of drill holes in our pelecypod samples is generally less than 10, we have only a few reliable estimates of the effectiveness of shells against drilling. Nevertheless, it is clear from Table 2 that several Japanese species, especially *Pseudocardium sachalinense* and *Peronidia venulosa,* have an effective armor defense against drilling, as inferred from the ratio of incomplete drill holes to the total number of holes. Comparably high values of 0.50 or higher have not previously been reported for Recent prey species, although those for Indonesian *Anadara* (*Tegillarca*) *granosa* (Linnaeus, 1758) drilled by muricaceans (effectiveness 0.41) and of *Stewartia floridana* (Say, 1822) drilled by naticaceans (effectiveness 0.35) come close (VERMEIJ, 1980b; KITCHELL *et al.,* 1981). The only species in which the effectiveness of the shell exceeds 0.50 are some thick-shelled Eocene and Miocene venerid and corbulid pelecypods (VERMEIJ, 1987).

The study of successful and unsuccessful predation makes possible the identification of prey characteristics that function to protect the prey against predation. In the sample of *Pseudocardium sachalinense* from Locality 2, however, we were unable to detect any difference in the position or size of complete and incomplete drill holes (Table 4).

The lack of difference in position between complete and incomplete holes in *Pseudocardium sachalinense* recalls the situation in a sample of *Anadara granosa* from the Indonesian island of Halmahera, in which complete and incomplete muricacean holes had a common distribution near the posterior end of the shell (VERMEIJ, 1980b). For these two species, therefore, we are unable to identify specific features of armor that serve to protect the prey against drilling despite the high overall effectiveness of armor. By contrast, incomplete holes in *Stewartia floridana* are concentrated in the distinctly thickened central portion of the valves (KITCHELL *et al.,* 1981). In the Australian limpet *Patelloida alticostata* (Angas, 1865), drilling success is dictated by how snugly the rim of the muricacean predator's aperature fits over the prey's shell; holes are more often incomplete in those parts of the shell where the fit is poor (BLACK, 1978). Incomplete holes in most fossil and living

corbulid pelecypods are concentrated in the left valve (DE CAUWER, 1985). In these clams, an internal organic shell layer seems to prevent drilling predators from completing their holes (FISCHER, 1963; LEWY & SAMTLEBEN, 1979). Finally, PALMER (1982) showed that unsuccessful attempts by muricaceans (species of *Nucella*) to drill barnacles tended to be within plates as compared to the sutures between plates. In all these cases, the differences in distribution between complete and incomplete holes point to features of armor (thick shell wall, rough or uneven surface, presence of organic layer, and limited number and length of sutures between external skeletal elements) that function effectively to prevent successful drilling.

Concluding Remarks

Because it is so readily quantifiable in Recent as well as fossil samples of shells, drilling is perhaps the best understood form of predation on mollusks. Reasonably robust geographical and temporal patterns of successful and unsuccessful drilling are being uncovered, and estimates of the great variation at small spatial scales are becoming available. Yet, many important questions remain unanswered, and large areas of the world's marine biota remain unsurveyed with respect to drilling predation. Is edge-drilling faster than side-drilling? What accounts for the equatorward increase in drilling predation in turritellid gastropods? Is the decrease in complete and incomplete drilling in pelecypods from north-temperate latitudes to the tropics mirrored in the southern hemisphere? Do escape and lack of detection play a greater role as anti-drilling attributes toward low latitudes? With continued study, the role of drilling in the evolution of shell-bearing mollusks will become increasingly well understood.

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Limpet Radulae: The Relationship Between Intertidal Height and Radula Length in Temperate and Tropical Limpets

by

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Abstract. The relationship between radula length and height occupied intertidally was investigated in several species of limpets in British Columbia and Barbados. Radulae were significantly longer in high-level individuals as compared with low-level ones in *Tectura persona, Acmaea jamaicensis,* and *A. leucopleura,* but not in *Lottia digitalis* or *T. scutum.* The extent of such intraspecific difference in radula length may be related to the degree of homesite fidelity exhibited by a species which, in turn, limits the feeding opportunity of high- and low-intertidal members of a population. Results of a field translocation experiment to test the effect of feeding time on radula length led to inconclusive results, but a parallel laboratory tide-tank experiment offered support for the idea that food availability and feeding opportunity may be important in regulating radula length.

INTRODUCTION

Limpet radulae are best known for their taxonomic importance, but are also of ecological interest. Radula fraction (defined as radula length over shell length; FISCHER-PIETTE, 1935) was initially investigated as a taxonomic character in *Patella* spp. by EVANS (1947) and BRIAN & OWEN (1952). However, the classificatory value of this ratio was dismissed in the latter study owing to its marked intraspecific variation and an apparent correlation between radula fraction and the animal's intertidal position. BRIAN & OWEN (1952) showed that the radula fraction of high-level *P. vulgata* at five sites on the west coast of Great Britain was greater than that of lower-level conspecifics, confirming a pattern reported earlier by EVANS (1947), and EBLING *et al.* (1962), for *Patella* spp. and later documented by RAO & GANAPATI (1967) for *Cellana radiata.*

Intertidal-level differences in radula fractions of limpets, as defined by the above authors, can represent the combination of two contrasting tendencies: (1) a decrease in shell length with increasing intertidal height, possibly caused by desiccation stress (ORTON, 1932; MOORE, 1934; EBLING *et al.,* 1962; VERMEIJ, 1973; SIMPSON, 1985) and (2) an increase in radula length with increasing tidal height owing to a presumed decrease in radula wear as limpets at higher levels have less immersion time in which to feed. Neither tendency individually caused statistically significant differences in shell or radula length in the study of *Patella vulgata* by BRIAN & OWEN (1952), and there has been dispute among past investigators as to which factor contributes most to an observed tidal height-related change in radula fraction.

It is the purpose of the present study to reinvestigate the relationship between intertidal height and radula fraction in limpets. To this end a correlate of radula length that is not independently affected by tidal height was sought as a replacement for shell length in the definition of radula fraction. Possible correlates such as shell height, width, volume, and dry weight of soft tissues were investigated for the limpet *Tectura persona* in British Columbia. The relationship between intertidal height and radula length was studied in this species, in *Lottia digitalis,* and in *T. scutum,* as well as in the Caribbean species *Acmaea leucopleura* and *A. jamaicensis.* The effect on radula length of reciprocal translocations of limpets from high to low intertidal positions was studied in *T. persona* using field cages and a laboratory tide-tank. Finally, the relation of radula length to extent of vertical movement undertaken by a limpet species was investigated in three acmaeid species in

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Barbados, *A. leucopleura, A. jamaicensis,* and *A. antillarum,* which exhibited various degrees of homesite "attachment." (Note: there is confusion regarding the taxonomic status of Caribbean limpets [D. Lindberg, personal communication], especially with regard to possible synonymy of *A. leucopleura* and *A. jamaicensis.* However, in the present study the three putative species occupied different habitats, lived at different intertidal heights, were of different size ranges, and showed differences in behavior especially with respect to homing.)

MATERIALS AND METHODS

Habitat Descriptions

Limpets were collected at two sites in British Columbia (January–March 1987) and at one site in Barbados, West Indies (May 1987). *Tectura persona* was collected at Lighthouse Park near Vancouver, British Columbia, a semi-protected rocky area consisting of tumbled boulders extending from a vertical rock-face. *Lottia digitalis* and *T. scutum* were collected from a site near the Bamfield Marine Station on the west coast of Vancouver Island, British Columbia. In this region *L. digitalis* occupied a wave-exposed vertical rock-face, while *T. scutum* was found among tumbled rocks in a more sheltered area. At all British Columbia sites the food available to the limpets consisted of benthic diatoms and small epilithic red and green algae, more abundant at the lower intertidal levels during summer (see also PHILLIPS, 1981), but more evenly distributed throughout the intertidal zone during winter when a rich diatom growth was evident. The limpets were unevenly distributed. At the more wave-exposed Bamfield site, the population of *L. digitalis* was denser at higher intertidal levels. *Tectura persona* at Lighthouse Park were also in greatest abundance at higher intertidal levels. Larger individuals of both species tended to be found at higher parts of the distribution, and smaller ones at lower parts. This may represent an age segregation of the population, as has been noted in other studies (*e.g.,* BREEN, 1972). To eliminate size (age) effects as far as possible in the present study, we attempted to select animals of similar size ranges from the two intertidal levels. This was possible with most species, except *L. digitalis,* where the size disparity between high- and low-level inhabitants was greater. In any case, such size discrepancies were ultimately accounted for by a factoring design in the ANOVA which compared different sets of animals at a common size. The overall vertical range occupied by each population was as follows: *T. persona* (2.6–4.3 m above chart datum), *L. digitalis* (2.9–4.5 m), and *T. scutum* (1.0–2.9 m).

The tropical limpets *Acmaea jamaicensis, A. leucopleura,* and *A. antillarum* were collected from a coral limestone breakwater wall and adjacent boulder riprap at Six Men's Bay, on the west coast of Barbados. At this site, food available to the limpets consisted of diatoms, algal sporlings, and other unicellular and filamentous green algae. The populations were distributed from about 0.20 to 0.85 m above chart datum, with *A. antillarum* occupying the lower portion and *A. jamaicensis* and *A. leucopleura* the upper portion, with total tidal range on spring tides in this region being about 1 m. Precise demarcation of intertidal distributions was made difficult by almost constant wave splash, even on fairly calm days. The size distribution of the three species was nearly equal throughout their vertical ranges, although for *A. jamaicensis* larger individuals tended to be found at the lower part of the distribution and smaller individuals at the upper part.

The three acmaeid species in Barbados exhibited graded degrees of homesite fidelity, from *Acmaea leucopleura,* which occupied distinctive homesite scars conforming in size to their shell dimensions, to *A. jamaicensis,* which showed some site fidelity (to depressions in the rock, not their own scars), to *A. antillarum,* which showed no site fidelity. Observations were made on individual *A. leucopleura* and *A. jamaicensis* to assess the extent of daily movements in total distance and, for the latter species, in net vertical distance. Individual animals were identified through scratch marks (*A. leucopleura*) or distinctive natural markings or growths (*A. jamaicensis*) on their shells. For *A. leucopleura,* orientation markings scratched on the rock surface adjacent to the home scar in line with the mark on the shell were used as reference points to determine whether animals had made foraging excursions. A limpet was judged to have moved if it was found in a different orientation in its scar or in a different scar; this was a minimum estimate because some animals may have made undetected excursions by returning to the same scar and orientation. In the case of *A. jamaicensis,* which lived on a vertical part of the rock wall, two reference nails were driven into the rock on which was hung a sheet of clear plastic where locations of animals were marked. Observations on site fidelity of *A. leucopleura* and *A. jamaicensis* were made on successive low tides over 15- and 10-day periods, respectively.

Radula Lengths

Lengths of radulae were recorded for most species from animals collected at their highest and lowest intertidal distributions. Where a species' distribution was exceptionally narrow as, for example, *Acmaea antillarum* in Barbados, animals were collected at a single tidal level. For a population of *Tectura scutum* at Bamfield, radula lengths were examined from a series of animals occupying different intertidal heights over a vertical range of 1.8 m.

Each limpet's radula was removed from the radula sac by pulling it out through an anterodorsal incision in the buccal mass. The intact nature of the organ was assured by the appearance of a clear end to the radula on which no cusps could be seen with a dissecting microscope. Radula length was taken as the total length procured by this technique. In addition to radula length, the following morphological characteristics were recorded from each dissected *Tectura persona*: (1) shell length, (2) shell width,

(3) shell height, (4) shell volume, and (5) dry tissue weight. Measures of body dimensions were done with vernier calipers. Weight-to-volume standardized sand was used to obtain shell volume. Dry tissue weight, including radula, was recorded for limpets removed from their shells and oven-dried to constant weight at 90°C. For the other limpet species, only shell length and dry tissue weight were determined. Although animals were starved for 2 days prior to dissection to clear their guts, some digested food remnants regularly remained in the posterior gut loops and were included, therefore, as tissue weight. A separate investigation showed that the magnitude of this error source was in fact small, the dried gut contents representing a mean of 1.6 ± 0.4 SE % of the total dry weight in high-level animals (n = 11, 40–320 mg dry tissue wt) and 2.8 ± 0.8 SE % in low-level animals (n = 12, 20–100 mg dry tissue wt).

Translocation Experiments

In order to assess the effect of a change in intertidal height on radula length a reciprocal translocation experiment was done in the field using *Tectura persona*. High intertidal-level animals were transferred to a low intertidal level and low animals to high. Control animals were maintained at their original intertidal heights. After a 10-week period (estimated to be long enough to allow the radula to change in length), the animals were dissected and radula length and body size data collected as before. Field cages, consisting of two mesh boxes (0.5 × 0.3 × 0.2 m height, aluminum mesh of 10-mm-opening size), were placed in the Lighthouse Park site 2.6 m above zero chart datum. Limpets were also barricaded into narrow, shallow crevices in the rock-face at 4.3 m tidal level, using similar aluminum mesh. Sixty animals were collected at each tidal height, divided into two groups of 30, and placed in the appropriate cages on rocks collected from the surrounding beach area. Thus, at each level, cages housed 30 animals from the high intertidal level and 30 from the low, with one set being the control, and the other, the experimental. After a 10-week period the animals were retrieved and their radulae removed.

In order to test more completely the assumption that radula wear is the main factor influencing radula length, an additional experiment was performed in a laboratory tide-tank. We hoped that the tide-tank would provide a more uniform environment than the field, a uniform environment in which all animals would feed off the same substratum which, owing to uniform illumination in the tank, would support similar types and amounts of algal growth. The experiment involved translocation of high-level *Tectura persona* to simulated high and low levels in the tank. The animals were kept in this tank on slate plates (25 × 25 × 0.5 cm thick) suspended at heights corresponding to their intertidal heights in the field. The laboratory tide-tank produced simulated semidiurnal tides of 1-m magnitude on a 24-h cycle (Carefoot, 1981). The vertical separation of the plates was 0.34 m, equivalent to a separation of 1.7 m in the field. Several 60-W fluorescent bulbs were suspended above and in front of the tide-tank to promote algal growth on the slate plates. Prior to introduction of the animals into the tank, the plates supported a visible growth of diatoms and, after being placed on the plates, animals were observed to feed on this growth during immersion. No attempt was made to monitor the intensity of illumination or, except in a qualitative way, to assess the production and consumption of algal food on the plates. The experiment involved 60 animals collected from a high intertidal position in September and divided into two subgroups of 30 animals each. One subgroup of high intertidal-level animals, representing the control set, was placed on high-level plates in the tide-tank (15 animals per plate); the other subgroup, representing the experimental set, was placed on low-level plates. Animals were sampled at time 0, and then after 3 and 7.5 weeks in the tide-tank. In this way, we hoped to learn something of the time sequence involved in length changes in the radulae.

Data Analyses

Stepwise linear and logarithmic multiple regression analyses were done on regressions of radula lengths versus shell length, shell height, shell volume, and dry weight in *Tectura persona* in an attempt to identify the size variate giving the best correlation with radula length. In so doing, we hoped to identify a correlate of radula length that was not as independently affected by tidal height to substitute for shell length in the previous definition of radula fraction, and thus to develop a better means of correcting measures of radula length for animal size.

Log-transformed high- and low-level radula lengths were compared within and between species using two- and three-way analyses of variance (ANOVA), respectively, and multiple comparison tests (MCT, $\alpha = 0.05$), with weight factored out. The use of a factoring design in the analysis allowed size ranges of animals to be compared directly without resorting to a size-corrected "radula fraction" as used in previous studies (Brian & Owen, 1952; Rao & Ganapati, 1967). Some covariance analyses (ANCOVA) of slopes of regression lines were also performed.

RESULTS

Regression statistics for the relationship of radula length to various size dimensions of the body (shell length, width, height, and volume, and dry tissue weight) in *Tectura persona* are given in Table 1. Also included are regression statistics for the relationship of radula length to dry tissue weight for *Lottia digitalis*, *T. scutum*, *Acmaea leucopleura*, *A. jamaicensis*, and *A. antillarum*. Because it was initially unclear whether radula length would scale linearly with weight and volume dimensions, or whether a non-linear function would give the best fit, some of the data were fitted to both linear ($y = a + bx$) and logarithmic ($\log y$

Table 1

Regression statistics for the relationship of radula length to various shell parameters and dry tissue weight for several species of limpets. Linear regression equation: $y = a + bx$; logarithmic regression equation: $\log y = \log a + b \log x$.

Species	Intertidal position	Parameter measured	Regression type	a†	b	r
Tectura persona	High	Shell length	Linear	−0.98	1.89	0.83
		Shell width	Linear	−4.56	2.63	0.84
		Shell height	Linear	5.39	4.32	0.85
		Shell volume	Linear	23.64	16.64	0.78
			Logarithmic	0.64	0.38	0.84
		Dry weight	Linear	24.54	0.10	0.77
			Logarithmic	0.87	0.35	0.83
	Low	Shell length	Linear	2.50	1.51	0.75
		Shell width	Linear	4.46	1.74	0.67
		Shell height	Linear	11.59	2.62	0.75
		Shell volume	Linear	22.34	10.90	0.78
			Logarithmic	0.53	0.25	0.59
		Dry weight	Linear	21.37	0.09	0.78
			Logarithmic	0.89	0.31	0.77
Lottia digitalis	High	Dry weight	Linear	13.28	0.06	0.68
			Logarithmic	0.72	0.29	0.69
	Low	Dry weight	Linear	11.81	0.08	0.85
			Logarithmic	0.74	0.28	0.87
Tectura scutum	Mixed	Dry weight	Linear	27.67	0.04	0.81
			Logarithmic	0.86	0.21	0.65
Acmaea leucopleura	High	Dry weight	Linear	10.48	0.09	0.64
			Logarithmic	0.80	0.22	0.66
	Low	Dry weight	Linear	8.35	0.10	0.82
			Logarithmic	0.68	0.26	0.85
Acmaea jamaicensis	High	Dry weight	Linear	9.29	0.10	0.57
			Logarithmic	0.81	0.19	0.63
	Low	Dry weight	Linear	8.51	0.09	0.61
			Logarithmic	0.74	0.20	0.70
Acmaea antillarum	Mixed	Dry weight	Linear	8.98	0.17	0.90
			Logarithmic	0.47	0.46	0.81

† For logarithmic regressions, a is given in log form.

$= \log a + b \log x$) equations. For *T. persona*, r values ranged from 0.77 (dry weight) to 0.85 (shell height) for high-level animals, and from 0.59 (log shell volume) to 0.78 (dry weight and shell volume) for low-level animals. Overall, low intertidal-level *T. persona* showed greater variability in radula lengths in relation to the correlates tested than did high-level animals regardless of whether they were linearly or logarithmically expressed. A stepwise multiple regression analysis of the linear values showed that shell height and dry tissue weight accounted for most of the variance in radula length in high-level *T. persona* (t values of 2.935 and 1.074, respectively, d.f. = 17; but only shell height was significant: $t_{0.05(2),\,\text{d.f. }17} = 2.110$), and shell volume and dry weight in low-level animals (t values of 3.165 and 4.741, respectively, d.f. = 17). A similar analysis on the logarithmic values resulted in no significant effect of any variable on radula length for high-level animals (t values <0.416, d.f. = 15, where $t_{0.05(2),\,\text{d.f. }15} = 2.131$), but a highly significant effect of dry weight in low-level animals ($t = 4.596$, d.f. = 17). Overall, then, dry weight accounted for the greatest effect on radula length of all parameters tested in *T. persona*. Also, because the correlation coefficients for logarithmic regressions of radula length and dry weight were mostly as high or higher than for the comparable linear regressions for all species, and because it would generally be expected that radula length would scale non-linearly with dry weight, the logarithmic relationship was accepted as the working model for *T. persona* and for the other limpet species in the present study.

In all instances where a limpet species showed strong homing tendencies (*Acmaea leucopleura* and *A. jamaicensis*) or remained at a relatively constant intertidal height (*Tectura persona*), radulae were longer in the high intertidal-level animals than in the low-level ones (Figure 1, Table 2; respective P values of <0.001, <0.001, and 0.01; ANOVA). For these three species, radula length of high-level animals was about 14% greater than that of low-level animals at a given weight. In comparison, neither *Lottia digitalis* ($P = 0.87$, ANOVA) nor *T. scutum* showed sig-

Table 2

Radula lengths in high- and low-intertidal limpets. The "common weight" is the factored dry tissue weight at which the ANOVAs were performed between high- and low-intertidal groups of the same species. Slopes of radula lengths versus dry weight of tissues did not differ significantly between high- and low-level groups for any species ($P > 0.50$, ANCOVA).

Species	n	Intertidal position	Height above chart datum (m)	Animal weight ($\bar{x}$ dry mg ± SE)	Common weight (dry mg)	Radula length at common weight (mm)	P (ANOVA)
Tectura	20	High	4.3	67.2 ± 12.7	57.0	30.5	0.01
persona	20	Low	2.6	71.3 ± 12.3		27.2	
Lottia	25	High	4.5	90.8 ± 4.2	61.4	17.3	0.87
digitalis	25	Low	2.9	45.5 ± 3.6		17.4	
Acmaea	25	High	0.50	31.0 ± 1.7	29.4	13.3	<0.001
leucopleura	25	Low	0.20	33.0 ± 3.2		11.5	
Acmaea	25	High	0.85	15.8 ± 1.2	17.3	11.1	<0.001
jamaicensis	25	Low	0.20	22.6 ± 2.1		9.7	

nificant intertidal-height effects (data for *T. scutum* presented in Figure 2 as the relationship between the ratio of radula length over dry tissue weight, to intertidal height occupied). Slopes of regressions of radula length on dry tissue weight did not differ significantly ($P > 0.50$, ANCOVA) between the high- and low-level groups for any species. Therefore, the differences shown by ANOVA are not due to size (age) effects, but rather to some other effect(s) (*e.g.*, intertidal height).

Observations on the extent of homesite fidelity in *Acmaea leucopleura* and *A. jamaicensis* showed that while neither species moved very much, the former may have been more strongly "site-attached" (Table 3). Movements by *A. jamaicensis* were from one small depression in the rock to another, while movements of *A. leucopleura* were on and off "homesite" scars. Some *A. leucopleura* occupied more than one scar and movements were limited to these. Sixty-five percent of all observed day-to-day movements by this species terminated on the same scar, 35% on an alternative scar. Mean vertical displacements of the two species did not differ significantly from zero, nor did high- and low-level groups of *A. jamaicensis* differ significantly from one another (Table 3). Although precise data on vertical movements of *A. leucopleura* could not be obtained because of rough-water conditions and irregular rock topography, it was apparent from observations of marked individuals that vertical displacements were smaller in this species than in *A. jamaicensis*. Each species had radulae that were significantly longer in high intertidal-level animals (Table 2). However, the difference in radula lengths between high and low individuals was somewhat greater in *A. leucopleura* than in *A. jamaicensis* (16 and 14% differences, respectively), possibly reflecting the difference in homesite fidelity of the two species. Unfortunately, vertical movements of the low intertidal-level-inhabiting *A. antillarum* could not be monitored owing to difficulty in marking and, later, in locating individuals. Our observations, however, indicated that this species was much more free-ranging in its low intertidal-level habitat than the other two. The radula length in this species was 14.1 mm ($n = 21$), somewhat greater than in *A. leucopleura* (12.2 mm, $n = 50$) and *A. jamaicensis* (11.5 mm, $n = 50$) at a common dry tissue weight of 30 mg (determined from regression equations).

The results of the translocation experiments on *Tectura persona* are given in Table 4. As predicted, change in intertidal height had a highly significant effect on radula length in this species ($P < 0.001$, ANOVA). The most obvious effect was on radula lengths of high- and low-level control animals, with the former possessing radulae about 15% longer than the latter (46.2 and 40.0 mm, respectively, measured at the common dry tissue weight of 148 mg at which the ANOVA was performed; $P < 0.05$, MCT). However, the predictions that radula lengths would be decreased through translocation of high-level animals to

Table 3

Extent of movements of acmaeid limpets in Barbados resulting in returns to homesite scars or depressions, and net daily displacements after feeding excursions over a high-tide cycle. Individuals of *Acmaea jamaicensis* were divided into high and low intertidal-level groups (separated here by a vertical distance of 30 cm) and were observed over a 10-day period; individuals of *A. leucopleura* were observed over a 15-day period.

	Acmaea jamaicensis		*Acmaea leucopleura*
	High	Low	
n	5	4	11
Total no. of observations	50	40	130
Total no. of moves	11	11	70
Daily displacement			
Total ($\bar{x}$ cm ± SE)	0.8 ± 1.2	0.7 ± 1.5	1.6 ± 2.3
Range (cm)	0–4.3	0–13.3	0–8.2
Vertical ($\bar{x}$ cm ± SE)	−0.1 ± 0.7	0.5 ± 1.3	—

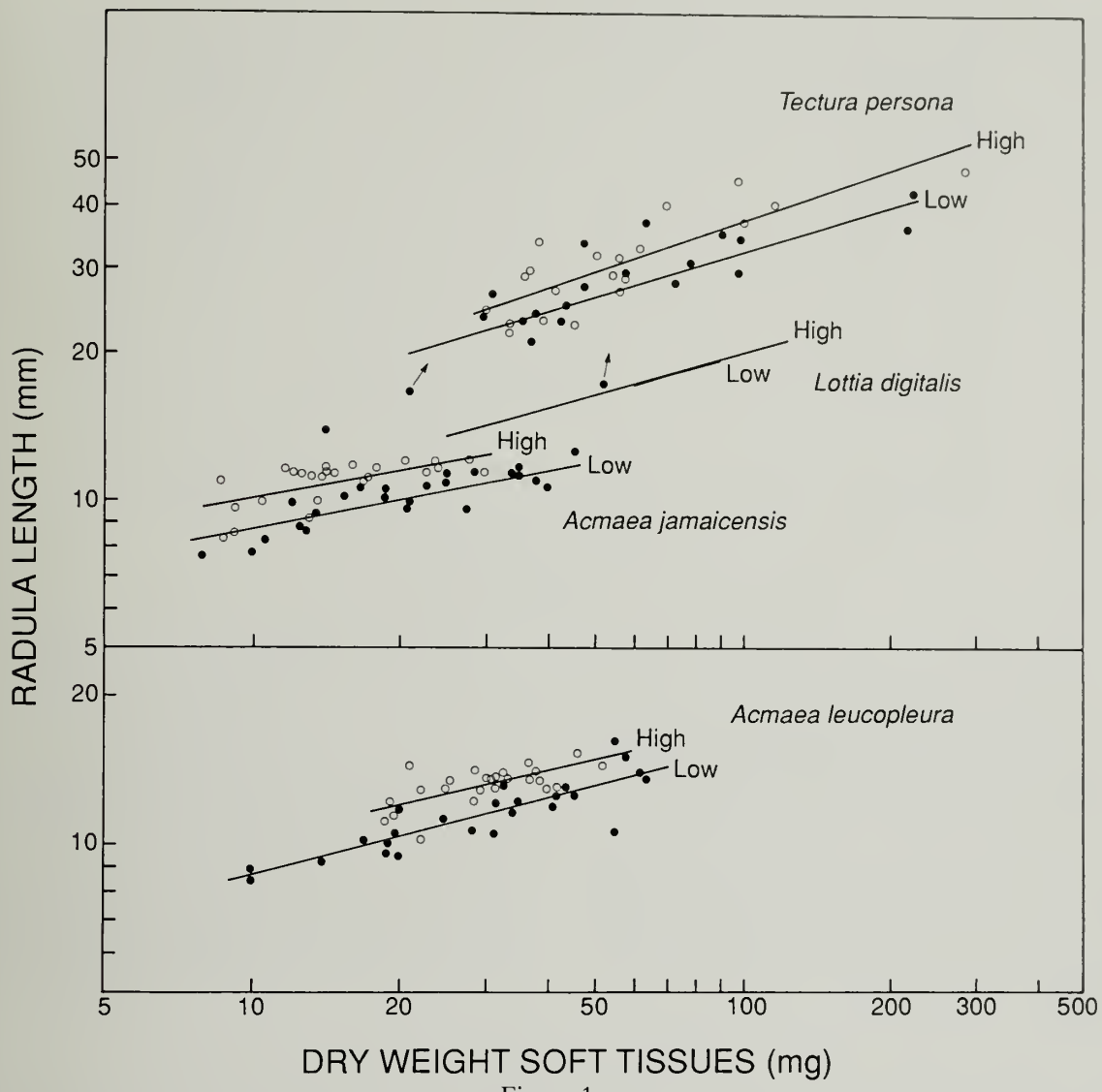

Figure 1

Comparison of radula lengths in high and low intertidal-level *Tectura persona, Lottia digitalis, Acmaea leucopleura,* and *A. jamaicensis*. High- and low-level data sets differ significantly for *T. persona* (F-ratio = 6.6, P = 0.01, ANOVA), *A. jamaicensis* (F-ratio = 18.7, $P < 0.001$, ANOVA), *A. leucopleura* (F-ratio = 33.6, $P < 0.001$, ANOVA), but not for *L. digitalis* (F-ratio = 0.03, P = 0.87, ANOVA); n = 20 for each set of *T. persona* and 25 for each set of each of the other species. Points omitted from *L. digitalis* regressions for clarity. Regression statistics for these curves are given in Table 1. Slopes of the regressions are not significantly different for any data set ($P > 0.50$, ANCOVA).

low, and increased through transfer of low ones to high, were not supported by the results. No significant effect on radula length was shown in low-level animals moved to a high level for 10 weeks (42.7 mm radula length as compared with 40.0 mm in the controls; $P > 0.05$, MCT), and high animals transferred to a low level for the same length of time unexpectedly showed a significant increase in radula length (53.0 mm after 10 weeks as compared with the control value of 46.2 mm; $P < 0.05$, MCT). Neither control set differed significantly with respect to radula length from uncaged animals at the same tidal height at the end of the 10-week period (uncaged low = 41.3 mm and uncaged high = 44.5 mm, for animals of 148 mg dry tissue weight; $P > 0.20$ for each comparison; ANOVA). We concluded from this that there were no significant cage effects on radula lengths.

The results of the tide-tank experiment to assess the effects of time on change in radula length (Table 4) showed that high-level animals, when transferred to a low level, apparently underwent a shortening of their radulae until,

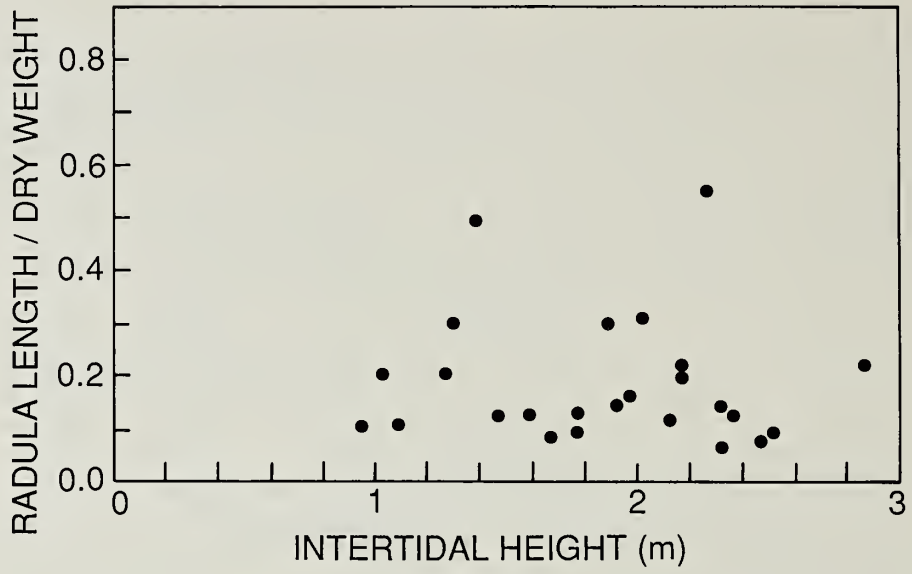

Figure 2

Relationship of the ratio of radula length over dry weight of soft tissues, to intertidal height occupied, in *Tectura scutum* from the west coast of British Columbia. Slope of the regression (b = 0.003) is not significantly different from zero ($P > 0.20$; t-test).

after 3 weeks, their radulae were significantly shorter than those of the controls (63.3 as compared with 73.0 mm, respectively; $P < 0.05$, MCT; measured at a common dry tissue weight of 440 mg at which the ANOVA was performed). However, after 7.5 weeks at a low level in the tide-tank, radula lengths of the experimental animals did not differ significantly from those of the controls (72.8 and 76.6 mm, respectively). The control animals showed some non-significant variation in radula lengths over the 7.5-week experiment (73.0–76.6 mm; $P > 0.05$, MCT).

DISCUSSION

Radula fraction, as defined by FISCHER-PIETTE (1935), has been frequently used as a means of comparing radula lengths in different-sized limpet species (ESLICK, 1940; BRIAN & OWEN, 1952; RAO & GANAPATI, 1967), variation in size supposedly being accounted for by using shell length as a correction factor. However, multiple regression analyses in the present study suggest that weight correction may more adequately ensure comparability of radula

Table 4

Effect of change in intertidal height occupied on radula lengths in the limpet *Tectura persona*. Translocation experiments were done using cages in the field and slate plates suspended at different "intertidal" heights in a tide-tank in the laboratory. "High" animals were collected from 4.3 m above zero chart datum and "low" animals from 2.6 m. Field cages were positioned at corresponding intertidal locations. Slate plates in the laboratory tide-tank were located at equivalent intertidal positions ("high," 0.89 m; "low," 0.55 m). The "common dry weight" is the factored dry tissue weight at which the ANOVAs were performed between high- and low-intertidal groups in order to eliminate size effects. Radula-length values were taken from the regression plot of radula length versus dry tissue weight for each set of data at the common weight indicated; n values are given in parentheses.

Study location	Season	No. weeks treatment	Common weight (dry mg)	Radula length (mm) after treatment: High kept at high: Control	High kept at low	Low kept at low: Control	Low kept at high
Field	Autumn	10	148	46.2 (18)	53.0 (18)	40.0 (18)	42.7 (11)
Tide-tank	Summer–autumn	0	440	74.5 (10)	73.9 (10)	—	—
		3	440	73.0 (12)	63.3 (8)	—	—
		7.5	440	76.6 (25)	72.8 (16)	—	—

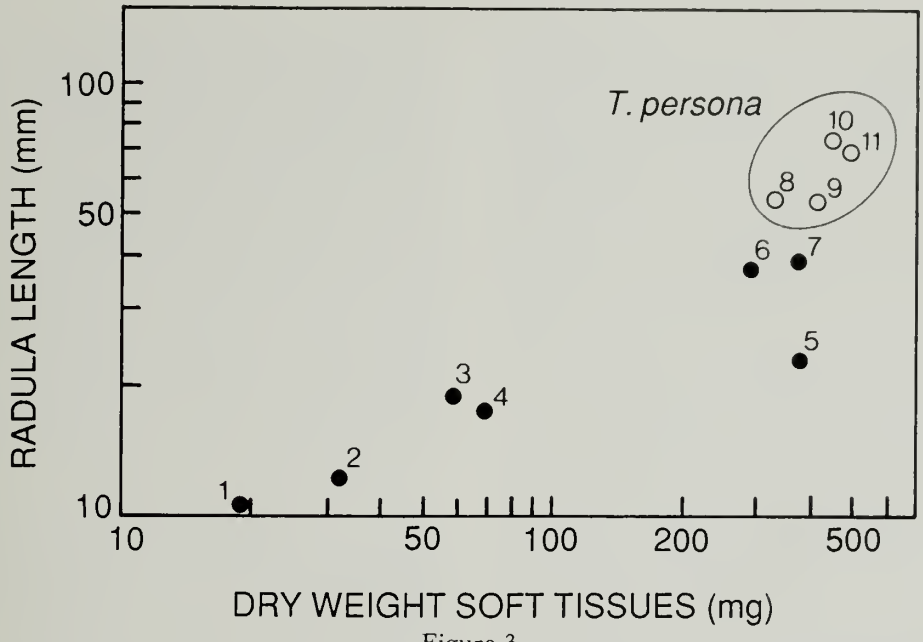

Figure 3

Relationship of radula length to dry tissue weight in several acmaeid and lottiid limpets from the west coasts of British Columbia and Barbados. Only large individuals from the upper portion of the intertidal range were chosen. Numbers by each point indicate the species, *n* value and, for species not part of the present study, geographical location as shown below. Numbers 8–11 represent populations of *Tectura persona* from different geographical areas in British Columbia. 1: *Acmaea jamaicensis*, *n* = 25; 2: *A. leucopleura*, *n* = 25; 3: *A. antillarum*, *n* = 25; 4: *Lottia digitalis*, *n* = 25; 5: *L. pelta*, *n* = 50 (DEHNEL, 1978); 6: *Tectura scutum*, *n* = 25; 7: *T. scutum*, *n* = 50 (DEHNEL, 1978); 8: *T. persona*, *n* = 25, Bamfield, B.C.; 9: *T. persona*, *n* = 25, Lighthouse Park, B.C.; 10: *T. persona*, *n* = 25, Botanical Beach, B.C.; 11: *T. persona*, *n* = 50, Bowen Island, B.C. (DEHNEL, 1978).

lengths than length correction, at least in *Tectura persona*. In a study of morphological variation in Pacific coast limpets, part of which included a comparison of radula length to various body dimensions, DEHNEL (1978) also concluded that weight of body tissue was a more accurate measure of animal size than shell length.

Radula length is a variable component both within (BRIAN & OWEN, 1952; RAO & GANAPATI, 1967) and between limpet species. Its magnitude may change in response to, or be correlated with, environmental factors such as intertidal height, desiccation, and geographical location. The variability in radula length between species is illustrated in a comparison of radula length versus dry tissue weight in a variety of lottiid and acmaeid limpets from the west coast of North America and Barbados (Figure 3). These data were taken from various literature references and from collections of *Tectura persona* around the British Columbia coast. They include only large animals at the high parts of their intertidal ranges. They show not only a wide scatter in weight-corrected radula lengths among the different species, but also some marked geographical differences. For example, at a common dry tissue weight of 425 mg, radula lengths of several populations of *T. persona* differ by as much as 37%. Thus, radula length seems to be a species-specific characteristic that can show striking geographical differences within a species. Effects on radula wear that might produce such differences include feeding rate, type of food eaten, substrate texture, and hardness of the radula cusps (see RUNHAM & THORNTON, 1967). Food abundance and availability, which vary with intertidal height both within and between geographical areas, may also be important. At present, there is little knowledge of how these factors affect radula wear in limpets.

The results of the present study suggest that the radula-lengthening effect of increased intertidal height may be a species-dependent tendency relating to how strictly individual limpets remain in a certain intertidal position. Differences in weight-corrected radula length were highly significant in *Acmaea leucopleura* and *A. jamaicensis*, species that demonstrate a high fidelity to "homesite" locations. To a lesser degree, significant differentiation in radula lengths was also exhibited by high- and low-level *Tectura persona*. Although this species is not generally considered a homing one (VILLEE & GROODY, 1940; BRANCH, 1981), daily movements appear to be slight (unpublished observations) and are mostly in the horizontal plane (VILLEE & GROODY, 1940). *Tectura persona* thus appears to occupy a relatively constant position on the shore. Similar observations have been made on *Patella vulgata* (BRIAN & OWEN, 1952; EBLING *et al.*, 1962; VERMEIJ, 1972), a species that also exhibits differences related to intertidal height in relative radula length. In comparison, no significant difference in weight-corrected radula length was shown by high-

and low-level *Lottia digitalis* (Table 2). This species shows no (Villee & Groody, 1940; Haven, 1973) or only slight (Frank, 1964; Galbraith, 1965; Miller, 1968; Breen, 1971) homing tendencies and, in addition, shows dispersal in response to crowding (Frank, 1965; Breen, 1972), moves vertically in response to tides and wave splash (Miller, 1968; Frank, 1965), and undertakes seasonal vertical migrations (Frank, 1965; Haven, 1971; Breen, 1972). Similarly, differentiation of radula length with respect to intertidal height was lacking in a population of *T. scutum* (see Figure 2). This is a free-roaming species (Test, 1945) that moves into and out of tide-pools, thus confronting variable feeding opportunities, and it shows no evidence of homing behavior (Villee & Groody, 1940).

These patterns of differentiation in radula lengths support the argument advanced by Brian & Owen (1952) and later by Rao & Ganapati (1967) that a decrease in radula wear in animals that live consistently at high intertidal levels, and therefore possibly experience more restricted feeding time, is chiefly responsible for the increase in radula fraction from low to high intertidal levels. Limpets have generally been observed to feed only when immersed, when emersed but on wet surfaces, or when splashed by waves (Orton, 1929; Sutherland, 1970; Boyden & Zeldis, 1979; Kitting, 1979; Hulings, 1985), although foraging behavior is variable even within a species (Little & Stirling, 1985; Little *et al.,* 1988). The idea of decreased feeding time being chiefly responsible for increased radula-fraction in high intertidal-level limpets is supported by the observations of Koch (1949) on South African *Patella* spp. This author recorded higher length-corrected radula lengths in species inhabiting drier parts of the shore where feeding excursions were limited. Similarly, more rapid relative growth rates shown by several limpet species in the lower intertidal area as compared with the upper may possibly be attributed to more food and greater availability of foraging time in the lower regions (Fischer-Piette, 1935; Sutherland, 1970; Lewis & Bowman, 1975; Phillips, 1981).

The results of the tide-tank translocation experiment also suggest that feeding opportunity (including feeding time, food availability, and food attractiveness) may be important in controlling radula length. Thus, the shortening of the radula in high-level animals 3 weeks after transfer to a low-level position in the tide-tank may have been caused by rapid feeding in animals confronted with abundant food on the slate plates. With subsequent depletion of food, the radula was worn less and showed an increase in relative length. At the end of the experiment the slate plates were barren of food and dissections of animals showed that both high- and low-level sets had empty stomachs.

As attractive as this explanation may be, however, it is not supported by the results of the field experiment. Diatoms were abundant throughout the intertidal region in December (particularly at the high levels) at the termination of the field experiment, and dissections of freshly collected field animals revealed that most had full guts. The lengthening of the radula evidenced by high-level animals moved to a low level was not reflected in the low-level control group, which had radulae of similar lengths to uncaged field animals at the same intertidal level. Mortality rates were high (40–63% in all experimental groups; no size-specific mortality), suggesting that handling and other stresses may have been involved. Attempts to move limpets from their natural substrata to other locations, with either the same substrata or an artificial one in the laboratory, usually resulted in slow reattachment and high mortality. Thus, the most logical means of testing the influence of tidal height on radula length, namely to effect a change in radula length through a manipulation of tidal height, provided unclear results in this study.

Although the physical limits on radula growth in limpets are not known, an individual that is not using its radula (and, thus, presumably not wearing it away) may continue to produce a radula until a "radular capacity" is maximized. It appears that in large specimens of *Tectura persona* maximum "capacity" is approximately 2.5 times the shell length, a ratio comparable to that found in high-level *Patella vulgata* (Evans, 1947). This abundance of radula can be thought of as an investment to be drawn on under improved feeding conditions. At present, there are no reliable estimates of radula replacement rates for limpets (see Isarankura & Runham, 1968). However, if radula replacement rate is consistent regardless of wear, this may explain the marked tide-level differences in relative radula lengths in species such as *T. persona* and *Acmaea leucopleura,* whose extensive vertical ranges put part of each population into the high intertidal zone where opportunity for feeding is presumably lessened. Thus, the greater the tendency for limpets to remain at a specific height for extended periods, the greater will be the lengthening effect on the radula. Presumably, as suggested by the data from the tide-tank experiment, once food-deprived limpets resume normal feeding, radula wear increases and the extensive radula built up during deprivation is worn away.

This analysis will remain speculative until major questions can be answered relating to the effect on radula length of differences in feeding rate and, in turn, to the amount of food required to meet energy demands. Energy requirements of limpets are undoubtedly different at different intertidal levels (see McMahon & Russell-Hunter, 1977) and may vary seasonally. Food supply is known to vary seasonally in both type and amount, and these variations will affect feeding rates and, thus, radula wear. Fluctuations in the type and density of food and general patchiness in distribution of food may explain the low correlation coefficients between radula length and morphometric parameters exhibited by low-level (*i.e.,* more actively feeding) limpets (see data for *Tectura persona,* Table 1). Studies are now underway to determine the effect of intertidal position on feeding rates and radula replacement rates in *T. persona* to help answer some of these questions.

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Shell Form and Burrowing Performance in Gastropods from Pacific Panama, with Comments on Regional Differences in Functional Specialization

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Abstract. A study of the burrowing performance of 22 species of gastropods from Pacific Panama revealed that a smooth external shell surface and a large foot were associated with rapid burrowing, whereas a sculptured surface and a small foot (associated with a tall spire or a slender body whorl) characterized slow burrowers. Comparison with an earlier study of 33 gastropod species from Guam suggests that Indo-West Pacific species are more specialized in the development of shell characters related to both antipredatory resistance and burrowing despite the general incompatibility between these two directions of functional specialization.

INTRODUCTION

Infaunal burrowing gastropods have been a conspicuous element of communities on shallow-water tropical sandy and muddy bottoms since Late Mesozoic time (VERMEIJ, 1987). In order to trace the history and evolution of the burrowing habit in gastropods, it is desirable to establish a functional relationship between shell architecture and burrowing performance in living species. In a previous study (VERMEIJ & ZIPSER, 1986), based on 33 burrowing gastropod species from the island of Guam in the tropical Indo-West Pacific region, rapid burrowing was found to be associated with a large foot (and usually a large shell aperture or the ability to extend the foot over the shell) and with a smooth external shell surface. Slow burrowers tended to have a small aperture (associated either with a high spire or with a slender body whorl) and well-developed shell sculpture (especially spiral cords). Ratchet sculpture, in which the anterior slopes of spiral elements are less steep than the posterior slopes, enhance burrowing performance in some high-spired species (SIGNOR, 1983), but it is found typically in relatively slow burrowers. Among species with a slender body whorl, those of a wedge-shaped conical aspect may have a small advantage over more cylindrical types, but again species of this shape are usually slow. Most gastropods in Guam were found to be sluggish burrowers.

The present study was undertaken to determine if similar functional relationships apply to a taxonomically quite different assemblage of burrowing gastropods in the rich biota of Pacific Panama. A secondary objective was to ascertain if the assemblages from Guam and Panama differ with respect to the burrowing performances of their component species. There is reason to expect such a difference. Previous studies have suggested that antipredatory resistance (great retractability of the soft parts, a narrow or toothed aperture) is better developed in Indo-West Pacific than in tropical American infaunal gastropod assemblages (VERMEIJ, 1978; VERMEIJ *et al.*, 1980). Given that such resistance is usually associated with a small aperture and therefore with slow burrowing, it might be expected that

Table 1

Burrowing performances of Panamanian gastropods.

Species	N_i	N_t	BRI	AS	SH	Sculpture
Natica grayi Philippi, 1850	2	4	0.60 ± 0.20	—	1.09	smooth
N. unifasciata Lamarck, 1822	8	15	0.71 ± 0.26	—	1.17	smooth
Polinices uber (Valenciennes, 1832)						
Burrowing with cyclical movement	4	8	0.75 ± 0.20	—	1.23	smooth
Burrowing without cycles	2	4	2.20 ± 0.40			
P. panamensis (Recluz, 1844)	2	3	0.91 ± 0.06	—	1.07	smooth
Phalium centiquadratum (Val., 1832) juvenile	1	2	0.61	1.40	1.27	raichel
Strombina bicanalifera (Sowerby, 1832)	4	4	0	1.71	1.48	smooth
Northia pristis (Deshayes in Lamarck, 1844)	1	2	0.69	1.52	1.95	smooth
Cymatophos fusoides (C. B. Adams, 1852)	1	2	0.16	1.47	1.93	axial
Nassarius complanatus (Powys, 1835)	1	2	1.23	1.32	1.33	cancellate
N. luteostomus Broderip & Sowerby, 1829	5	10	0.41 ± 0.19	1.30	1.35	nodose
N. scabriusculus (Powys, 1835)	1	2	0.06	1.27	1.79	axial
Olivella semistriata (Gray, 1839)	7	13	0.57 ± 0.11	—	1.39	smooth
O. volutella (Lamarck, 1811)	4	7	0.72 ± 0.46	—	1.51	smooth
Agaronia testacea (Lamarck, 1811)	3	6	1.66 ± 0.93	—	1.24	smooth
Cancellaria mitraeformis Sowerby, 1832	2	4	0	2.85	1.50	cancellate
Conus mahogani Reeve, 1843	4	7	0.18 ± 0.05	10.7	1.24	smooth
Pilsbryspira aterrima (Sowerby, 1834)	1	2	0.21	3.32	1.84	axial
Terebra glauca Hinds, 1844	3	6	0.25 ± 0.06	1.38	2.99	cancellate
T. hancocki Bratcher & Burch, 1970	1	2	0	1.67	3.62	cancellate
T. puncturosa Berry, 1958	1	2	0	1.19	4.13	axial
T. robusta Hinds, 1844	1	2	0	1.64	3.95	axial
T. strigata Sowerby, 1825	1	2	0	1.45	2.95	axial

Key: N_i—Number of individuals. N_t—Number of trials. AS—Aperture shape: aperture length divided by aperture width. SH—Spire height: shell height divided by aperture height. BRI—Burrowing rate index: cube root of wet weight divided by time in seconds for complete burial.

a greater proportion of species in Guam are slow burrowers than in the Panamanian fauna.

MATERIALS AND METHODS

In February of 1986, we collected 22 gastropod species from Playa Venado and two beaches near the Smithsonian Tropical Research Institute's marine laboratory at Isla Naos, on the Pacific coast of Panama. Individual animals were held at the laboratory for one to two days in tanks with a bottom layer of sand and running seawater. We conducted the burrowing trials in a small aquarium containing seawater and a 5-cm layer of coarse sand (6% gravel-pebble fraction, 19% very coarse sand, 34% coarse sand, 27% medium sand, 8% fine sand, 4% very fine sand, and 3% silt by weight). This sand was roughly similar to that used in the trials at Guam, in which the coarse-sand and medium-sized-sand fractions were 56% and 46% by weight respectively (VERMEIJ & ZIPSER, 1986). The sand was covered with a thin film of water. For each trial, we placed an individual snail on the sand surface, and recorded burrowing time in seconds, starting with the first burrowing movements that the animal made with its extended foot. The trial was ended when the animal was completely buried or when no additional burrowing movements occurred for a period of at least one minute. Once the animal was either completely buried or had ceased moving, we extracted it, redistributed the sand in the aquarium, and placed the animal on the surface of the sand for a second trial. At the end of the second trial, we dried the animal's shell surface with a paper towel, took the wet weight of the animal in grams, and measured apertural and overall shell dimensions in millimeters. The wet weight inevitably included some water in the shell. We could have measured volume instead of weight in order to alleviate this potential source of error, but it would have introduced other errors; moreover, our previous work in Guam was also based on wet weight. We did not measure the apertural dimensions of olivids and naticids, because these snails extend the foot over the exterior surface of the shell; as a consequence, the limits of the aperture are ill-defined, and in any case do not correspond with foot size.

We evaluated burrowing performance by calculating the burrowing-rate index (BRI), defined by STANLEY (1970) as the cube root of animal mass (wet weight) in grams divided by burial time in minutes. This size-independent quantity makes possible comparisons among species varying in size, architecture, and provenance (see STANLEY, 1970, and VERMEIJ & ZIPSER, 1986, for further discussion and documentation).

RESULTS AND DISCUSSION

The relationship between shell form and burrowing performance observed in gastropods from Guam was also evident in the Panamanian fauna (Table 1). The 10 species

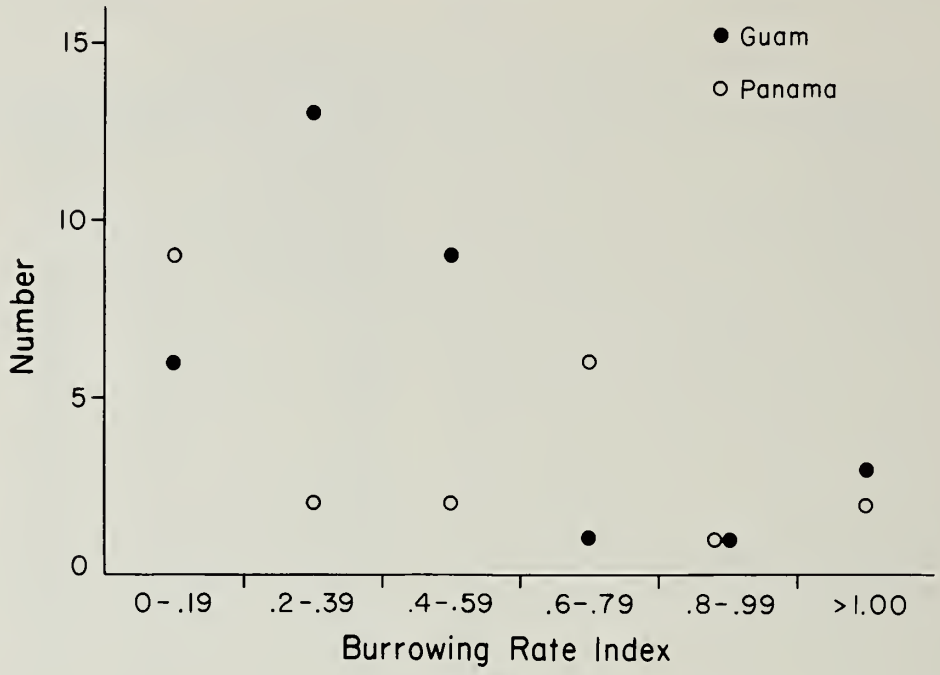

Figure 1

Comparison of burrowing rate indices of gastropods from Guam (closed circles) and Panama (open circles). Each circle represents the number of species in the indicated interval.

with smooth body whorls had significantly higher burrowing-rate indices (BRIs) than did the 12 sculptured species ($P < 0.05$, Mann-Whitney U-test). Only one of the 10 smooth-shelled species (*Strombina bicanalifera,* 10%) did not burrow completely during laboratory trials, as compared with five of 12 sculptured species (42%). Among the sculptured species, the one with ratchet sculpture (juvenile *Phalium centiquadratum*) ranked second highest in burrowing performance. If the 10 species represented by only a single individual are removed from the analysis, the difference in burrowing performance between the eight smooth and four sculptured species still holds ($P < 0.05$). The BRIs of the sculptured species all fall below the overall median of 0.49, whereas six of the eight smooth-shelled species fall above the median.

Small apertures were associated with slow burrowing. The three species with a narrow aperture (aperture length-width ratio 2.50 or higher) and without the ability to extend the foot over the shell were all poor burrowers; one (*Cancellaria mitraeformis*) did not burrow completely, and the other two (*Conus mahogani* and *Pilsbryspira aterrima*) had BRIs of only 0.18 and 0.21 respectively. The five high-spired species (all terebrids) had very poor burrowing abilities; four of the five failed to burrow completely, and the fifth (*Terebra glauca,* the only species with more than one representative) had a mean BRI of only 0.25, a value well below the median of 0.33 for the assemblage of 22 species.

Species that prey on mollusks or echinoderms were by far the fastest burrowers relative to their mass. These species, which belong to the families Naticidae, Cassidae, and Olividae, have a large foot, which is used both for burrowing and for capturing and suffocating prey (Marcus & Marcus, 1959; Hughes & Hughes, 1981; Hughes, 1985).

The spectrum of burrowing performances was similar in the Panamanian and Guamanian assemblages (Figure 1). The median BRI was 0.33 in both assemblages, and the number of fast burrowers (BRI 1.0 or higher) constituted 9% of the assemblages in both regions. Slow burrowers (BRI 0.25 or less) are slightly (but not significantly) better represented in Panama (11 of 22 species, 50%) than in Guam (10 of 33 species, 30%). If all species represented by only a single individual are removed from the analysis, the median BRIs in Panama and Guam are 0.49 (n = 12) and 0.37 (n = 22) respectively; rapid burrowers constitute 8% and 9% of the assemblages, and slow burrowers make up 42% and 32% of the assemblages from Panama and Guam respectively.

Despite the overall similarities, comparisons within families suggest that Panamanian species are somewhat poorer burrowers than are species from Guam. The three olivids from Panama all had lower BRIs than the two species from Guam. The five Terebridae from Panama had significantly lower BRIs than the six species from Guam. Only one of the five conids from Guam ranked below the Panamanian *Conus mahogani* in relative burrowing performance. The families Columbellidae and

Table 2

Incidence of traits related to burrowing performance in assemblages from Panama and Guam.

Trait	Panama		Guam	
	Number of species	Percent	Number of species	Percent
Smooth surface	10	45	14	42
Ratchet sculpture	1	4.5	4	12
Conical outline	1	4.5	7	21
Large aperture or foot	10	45	4	12
Narrow aperture or tall spire	8	36	31	94

Turridae were each represented in the two assemblages by one species; in both cases, the species from Panama had a lower BRI than did the species in Guam. No consistent difference in burrowing performance was, however, evident in the Naticidae and Nassariidae.

Although these comparisons are based on perilously small numbers of species and individuals, they suggest a difference in burrowing performance opposite to the one expected on the basis of the expression of traits related to antipredatory resistance in the two faunas. Even if further work should show that the within-family differences in burrowing performance between Guam and Panama are insignificant, the expected pattern that species in Guam should on average be poorer burrowers than those in Panama because of the greater development of antipredatory resistance is not borne out. Of the 33 species whose burrowing performance was evaluated in Guam, 31 (94%) showed clear specializations for morphological resistance to shell-breaking predators (that is, a tall spire, associated with deep retractability of the soft parts, and a narrow aperture). The corresponding number among the 22 Panamanian species was only eight (36%). These values (Table 2) are representative of the sand-dwelling molluscan biotas of the Indo-West Pacific and eastern Pacific respectively. The species from Guam have, to some extent, overcome the basic incompatibility between effective burrowing and effective armor. This is suggested by the higher incidence of several burrowing specializations there than in Panama (Table 2). This greater specialization is evident even within families. Many shallow-water Terebridae in the Indo-West Pacific region are smooth-shelled, whereas in the eastern Pacific such species constitute a small minority (VERMEIJ *et al.*, 1980). The same is true in the Nassariidae and Mitridae. Cone-shaped burrowers, in which a wedge-shaped leading edge is effectively combined with a narrow aperture, are found only among Conidae and the harpid genus *Morum* in the eastern Pacific, whereas in the Indo-West Pacific they occur in these groups as well as in the Mitridae, Turridae, and Strombidae. Ratchet sculpture is rare in tropical American gastropods. In the one species with this sculpture that we examined in the present study (*Phalium centiquadratum*), the ratchet effect occurs only in juvenile shells. In Indo-West Pacific faunas, ratchet sculpture is found in several species of *Rhinoclavis* (Cerithiidae), *Neocancilla* (Mitridae), *Terebra* (Terebridae), and *Pupa* (Actaeonidae), among others.

Despite the very limited scope of the present study, we believe that comparative studies of functional performance of species from different parts of the world are potentially informative. They may reveal unsuspected differences that in turn prompt further questions about the evolutionary conditions and events that have shaped modern faunas.

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Seasonal Variation in Brood Structure of *Transennella confusa* (Bivalvia: Veneridae)

by

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Abstract. The small venerid bivalve *Transennella confusa* inhabits protected, sandy mudflats along the central coast of California. Clams with broods were present throughout the year in a population from Pillar Point Harbor, San Mateo County. Brood structure is defined by two properties: (1) brood number, *i.e.,* the total number of embryos in a brood, and (2) the relative proportions of the different size classes of embryos. Seasonal variation was observed in both these measures of brood structure. Brood number is a function of adult length and no differences were found among the spring, summer, or fall samples; however, brood number was significantly lower in the winter. The relative proportions of developmental stages within a brood also varied seasonally, but not in the same manner as brood number. The proportion of the smallest size class of embryos was highest in the spring, lowest in the winter, and of intermediate values in the summer and fall. Based on these observations, and measurements of brood structure and adult population size structures of *T. tantilla* from False Bay, Washington, predictions are made relating the dynamics of brooding to adult population structure and recruitment patterns of *T. confusa* at Pillar Point Harbor, California.

INTRODUCTION

Since *Transennella confusa* Gray, 1982, was originally recognized as a species distinct from *Transennella tantilla* (Gould, 1852), no study on any aspect of the former's biology has been published. However, since that description, several studies of *T. tantilla* have documented various aspects of its ecology and life history—*e.g.,* brooding capacity (KABAT, 1985), seasonal variation in reproduction and growth (ASSON-BATRES, 1988), effects of trematode parasitism on reproductive output (KABAT, 1986), and effects of crab predation on population densities (ASSON-BATRES, 1986). Here we report on seasonal variation in reproduction of a population of *T. confusa* from central California and speculate on the association between the adult population dynamics and its reproductive biology.

The venerid bivalve genus *Transennella* is represented in the northeastern temperate Pacific by two species, *T. confusa* and *T. tantilla. Transennella tantilla* ranges latitudinally from Alaska south to Baja California whereas *T. confusa* is known only from Oregon to central California (fig. 14 in GRAY, 1982; KOZLOFF, 1983). Both species inhabit the top 2.5 cm of a variety of soft substrata, and range from the intertidal zone to depths of approximately 36 m (OBREBSKI, 1968; MAURER, 1969; GRAY, 1982). These species asynchronously brood their developing embryos and early juvenile stages in a pouch located between the inner demibranch and the visceral mass. Asynchronous, or sequential development, occurs when all or most developmental stages are represented in a single clutch; synchronous development occurs when all the members of a clutch are of the same developmental stage. Broods from both species can be found throughout the year (HANSEN, 1953; PAMATMAT, 1966; ASSON-BATRES 1988; this study).

We were specifically interested in observing how fecundity and the relative proportions of the different developmental stages varied over time. In this paper we quantify seasonal variation in both aspects of brood structure (*i.e.,* brood number and brood size structure) and relate these findings to adult population dynamics and recruitment.

MATERIALS AND METHODS

All specimens of *Transennella confusa* used in this study were collected from Pillar Point Harbor, California (37°30′N, 122°28′W; Figure 1) using a 1-mm sieve and identified based on the siphon and shell characteristics

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Table 1

Summary of *Transennella confusa* samples. The total sample number of dissections (Total) for each date is broken down into three categories: Females, Males, and Undetermined (sex). These are further divided into the non-parasitized (NP) and parasitized (P) categories for which are indicated the number observed in the category (n), the minimum (Min), maximum (Max), and average ($\bar{x}$) sizes in mm.

		Females				Males				Undetermined				
Date	Total	n	Min	Max	$\bar{x}$	n	Min	Max	$\bar{x}$	n	Min	Max	$\bar{x}$	
15 May '87	46	19	3.09	4.12	3.60	13	2.74	3.82	3.31	—	—	—	—	NP
		4	3.32	4.12	3.59	4	3.24	3.82	3.49	6	3.53	4.26	3.70	P
29 May '87	83	37	2.20	5.00	3.75	24	2.28	3.36	3.20	1	3.36	3.36	3.36	NP
		8	3.41	5.04	3.96	4	3.07	4.00	3.40	9	3.70	4.62	4.23	P
12 Jun. '87	43	21	3.10	4.62	4.03	14	2.73	4.70	3.54	—	—	—	—	NP
		3	3.41	4.36	3.76	1	3.79	3.79	3.79	4	4.10	4.98	4.51	P
1 Jul. '87	43	24	2.74	4.70	3.76	11	2.56	4.10	3.47	—	—	—	—	NP
		3	3.33	5.00	4.34	3	3.86	5.08	4.36	2	2.99	4.32	3.66	P
14 Jul. '87	45	20	2.88	5.22	4.01	22	2.76	4.92	3.75	—	—	—	—	NP
		2	3.52	4.51	4.02	—	—	—	—	1	5.09	5.09	5.09	P
27 Jul. '87	40	20	2.64	5.50	3.97	17	2.78	4.60	3.68	—	—	—	—	NP
		1	4.90	4.90	4.90	—	—	—	—	2	4.68	4.76	4.72	P
11 Aug. '87	40	30	2.32	4.78	3.44	7	2.56	4.36	3.63	—	—	—	—	NP
		—	—	—	—	—	—	—	—	3	4.54	5.16	4.78	P
8 Sep. '87	32	16	3.16	5.27	4.37	7	3.44	4.34	3.81	1	3.70	3.70	3.70	NP
		5	3.08	4.62	3.80	2	3.92	4.68	4.30	1	4.20	4.20	4.20	P
8 Oct. '87	37	23	2.56	5.04	3.79	9	2.78	3.84	3.28	1	3.16	3.16	3.16	NP
		2	3.52	3.60	3.56	—	—	—	—	2	3.36	3.82	3.59	P
8 Nov. '87	34	24	2.91	4.54	3.60	8	3.06	4.02	3.45	1	4.35	4.35	4.35	NP
		1	3.04	3.04	3.04	—	—	—	—	—	—	—	—	P
5 Jan. '88	26	21	3.21	5.15	3.92	3	3.07	3.21	3.16	—	—	—	—	NP
		—	—	—	—	1	3.66	3.66	3.66	1	3.76	3.76	3.76	P
19 Jan. '88	32	15	2.36	4.08	3.28	13	2.28	3.34	2.74	3	2.12	3.60	2.73	NP
		1	3.22	3.22	3.22	—	—	—	—	—	—	—	—	P
1 Feb. '88	44	20	3.04	4.31	3.72	11	2.72	3.79	3.17	1	2.54	2.54	2.54	NP
		9	2.76	4.16	3.54	1	3.21	3.21	3.21	2	3.54	3.83	3.69	P
20 Feb. '88	53	13	2.68	4.16	3.36	4	2.70	3.50	3.08	—	—	—	—	NP
		18	2.95	4.32	3.36	10	2.78	3.65	3.04	8	2.84	4.16	3.57	P
14 Mar. '88	26	7	3.62	4.16	3.83	2	3.50	3.62	3.56	—	—	—	—	NP
		14	3.52	4.64	4.00	1	4.06	4.06	4.06	2	3.32	3.39	3.35	P
12 Apr. '88	41	26	2.96	4.77	3.64	8	2.98	3.54	3.26	1	3.50	3.50	3.50	NP
		2	3.68	3.78	3.74	2	3.65	3.87	3.76	2	3.40	3.46	3.43	P
7 May '88	37	24	3.39	4.62	3.90	4	3.39	3.91	3.58	—	—	—	—	NP
		1	3.79	3.79	3.79	4	2.80	3.79	3.42	4	3.68	4.27	4.01	P
1 Jun. '88	59	30	2.53	4.77	3.64	15	2.31	4.07	3.18	—	—	—	—	NP
		4	3.85	4.85	4.37	2	3.48	3.67	3.58	8	3.12	4.92	4.13	P
Summary:	761	390	2.20	5.50	3.75	192	2.28	4.92	3.38	9	2.12	4.35	3.20	NP
		78	2.76	5.04	3.75	35	2.78	5.08	3.51	57	2.84	5.16	4.00	P

documented by GRAY (1982). Collections were made at a tidal level of approximately 0 m (MLLW) from a gently sloping, sandy mud tidal flat (see Table 1 for collection dates). Samples were transported back to the laboratory at the University of California, Berkeley, where each clam was isolated in a vial submerged in chilled seawater. This way if any clam "ejected" a juvenile from a brood, the juvenile was held in the vial and scored as part of the brood.

Because females were generally larger than males (Table 1), the largest individuals were always selected for dissection, as well as other individuals from other size classes. All dissections were accomplished within three days of collection. Before dissecting a brood from a clam, the dimensions (length, height, and width) of the adult were recorded to the nearest 0.05 mm using a dissecting microscope fitted with an ocular micrometer.

Each clam yields two brood masses, one from each demi-

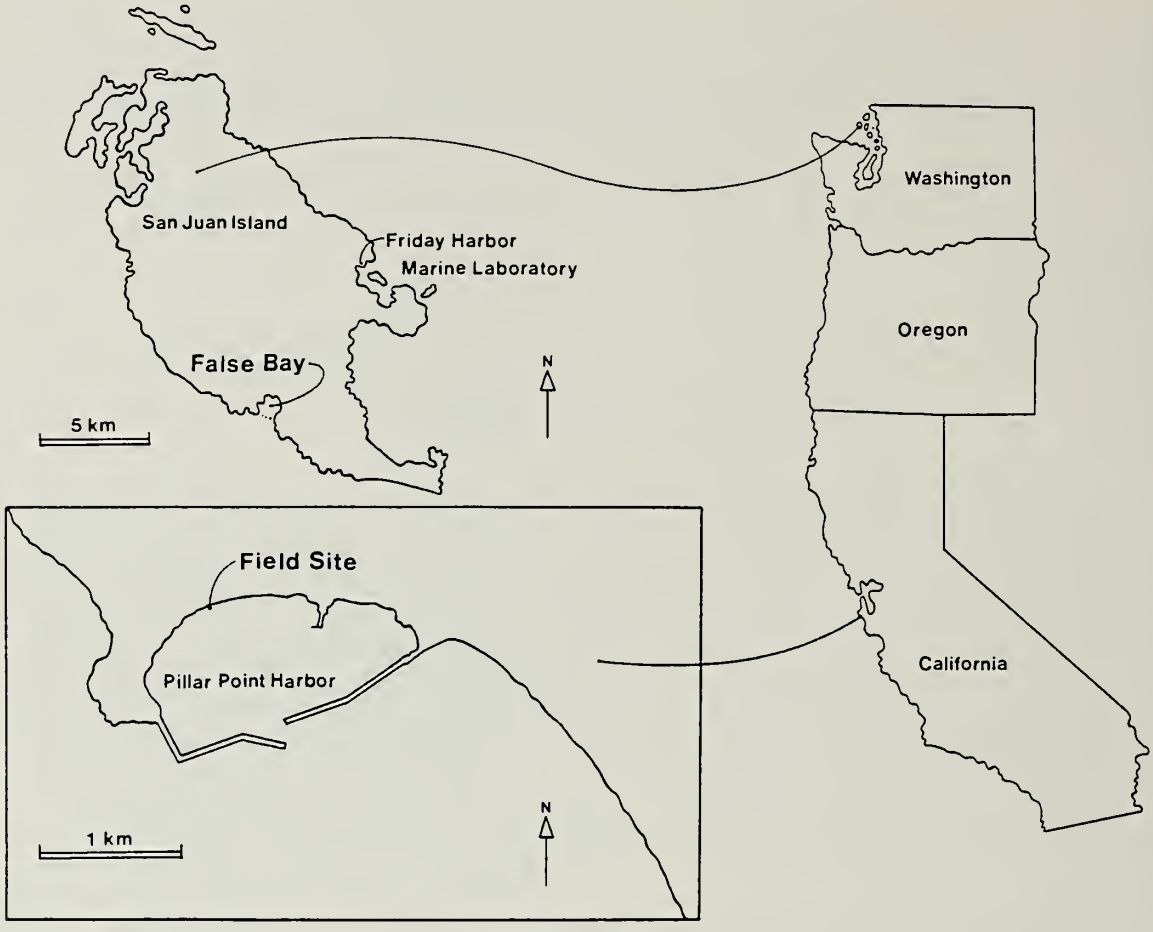

Figure 1

Map showing the location of our study site at Pillar Point Harbor, California, and False Bay, Washington. Only *Transennella confusa* is found at Pillar Point whereas only *T. tantilla* is found at False Bay.

branch. The brood mass extends dorsally underneath the umbo, where the smallest or youngest stages occur (as in figs. 2 and 3 in KABAT, 1985). A fine dissecting needle, hooked at the end, was "scooped" underneath the inside of the umbo and the brood mass was removed intact. The brood masses were separated and the number and sizes of the individual embryos and developing young were scored. Embryos were measured, using a dissecting microscope, along their longest dimension to the nearest 18 μm. For the later stages with fully formed valves this dimension is equivalent to adult length.

Two samples of *Transennella tantilla* were collected from False Bay on San Juan Island, Washington (48°29'N, 123°4'W; Figure 1; see PAMATMAT, 1968, for details of the study area). The summer samples were collected between 25 July and 10 August 1987 and the winter samples were collected 15 February 1988.

KABAT (1986) has shown that the reproductive output of *Transennella tantilla* at False Bay, Washington, is significantly reduced by trematode parasitism. Trematode parasitism has also been observed in *Transennella* at Lawson's Flat in Tomales Bay, California (OBREBSKI, 1968) which is approximately 80 km north of Pillar Point Harbor. Because trematode parasitism adversely affects estimates of fecundity, our analyses of brood variation include only data from nonparasitizd individuals. Parasitized individuals were recognized by the presence of cercariae or sporocysts in the mantle cavity or gonads. Females were identified by the presence of broods and males identified by the presence of sperm. An individual was scored as "undetermined" if neither a brood nor sperm were observed (Table 1).

RESULTS

The earliest stages of embryos in a brood are between 230 and 250 μm long and the latest are between 550 and 580 μm. Seasonal variation in reproduction can be estimated by the number of embryos present in a brood that are <300 μm long (Figure 2). The highest proportions of the

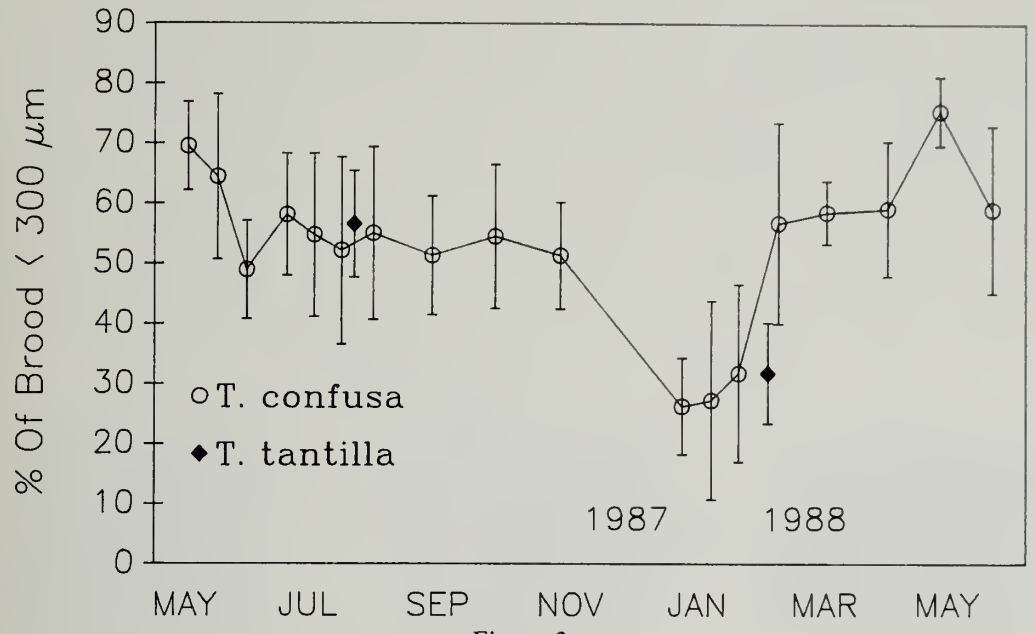

Figure 2

Estimates of reproduction as measured by the percent of the brood less than 300 μm long; points are means ±1 SD. Sample sizes varied from 36 (29 May 1987) to 7 (14 March 1988), and the mean sample size is 22 (SD = 6.5). The individuals of *Transennella confusa* are from Pillar Point Harbor, California, whereas those of *T. tantilla* are from False Bay, Washington.

earliest stages of development were found in the May dissections of both 1987 and 1988 (>65%). In both the June 1987 and June 1988 dissections this proportion dropped below 60%. Throughout the summer and fall of 1987 the "<300-μm stage" of the brood remained at approximately 50%. Reproduction dropped off in the winter as shown by the sharp decrease in the proportion of small embryos in the January and early February 1988 dissections (Figure 2).

The seasonal variation of reproduction in *Transennella confusa* was also evident in contrasting levels of brood number in the summer and winter. Between 1 July and 11 August 1987, 94 nonparasitized, brood-bearing clams were dissected; similarly, between 5 January and 1 February 1988, 56 clams were examined. Brood number was a function of adult size; however, brood number estimates were greater in the summer compared to the winter (Figure 3). There were no differences in the regressions of brood number versus adult length among the spring, summer, and fall samples (spring sample: combine May 1987 and 1988 dissections, $n = 80$; fall sample: 63 dissections between 8 September and 8 November 1987, $P < 0.05$, ANCOVA). In addition to seasonal variation in fecundity, we also observed seasonal differences in the relative proportions of developmental stages within the broods. As noted earlier, both the May 1987 and 1988 dissections were dominated by the smallest size class of embryos within a brood. This is illustrated in the histogram and accompanying photograph of a typical brood mass from the May 1988 dissections (Figure 4). In the summer and fall only about half of the brooded embryos were greater than 300 μm long. In contrast, winter broods were dominated by the larger size classes of embryos (Figure 4).

DISCUSSION

Based on linear regressions of brood number versus adult body length, Asson-Batres (1988) observed three distinct reproductive seasons of *Transennella tantilla* from Coos Bay, Oregon: summer, fall, and winter. For *T. confusa* at Pillar Point, we also found the lowest levels of brood number in the winter samples; however, unlike *T. tantilla* at Coos Bay, we were able to identify only two seasons of reproduction with respect to brood number (Figure 3).

Reproductive variation in studies of populations of brooders has been assessed in several different ways: by counting the number of embryos in a brood for different sizes of adults (Kabat, 1985), scoring brooders versus nonbrooders within a population over time (McGrath & O'Foighil, 1986), counting brood number for different stages of synchronous brooders (Strathmann *et al.*, 1984), or documenting seasonal variation in brood number for asynchronous brooders (*e.g.*, Asson-Batres, 1988). In order to rigorously quantify seasonal variation in the reproduction of asychronous brooders, the dynamics of the total brood structure must be considered.

Both the absolute number of embryos and the relative proportions of the different size classes of embryos deter-

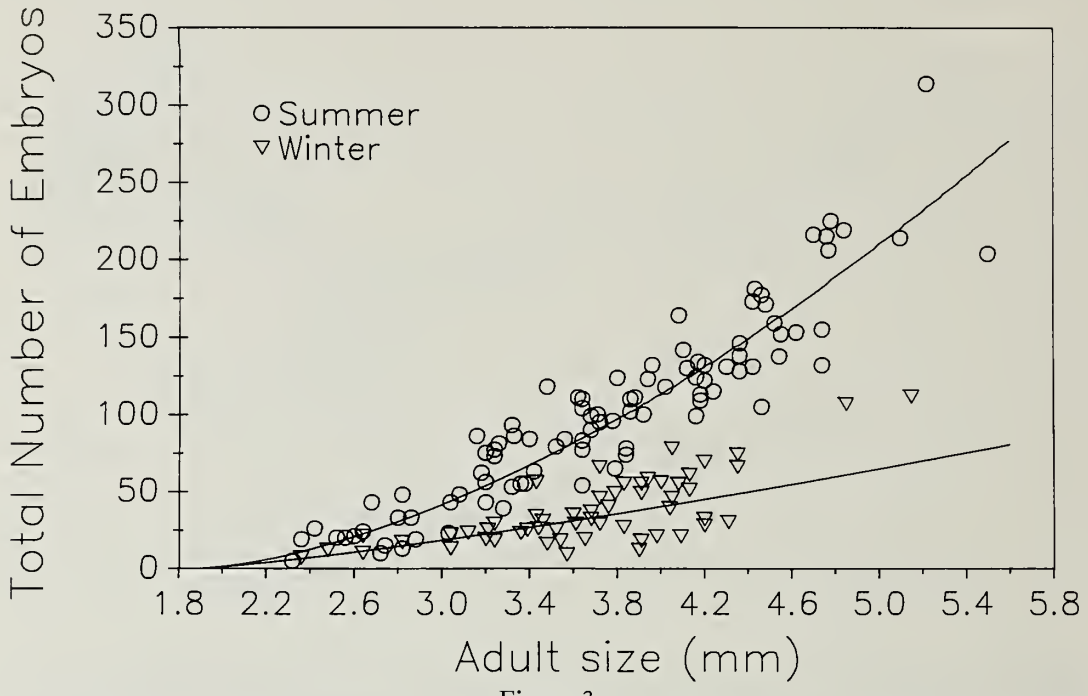

Figure 3

Transennella confusa. Allometric regressions of brood number as a function of adult length for the summer (dissections: 1 July–11 August 1987) and winter samples (dissections: 5 January–1 February 1988). Summer: Fecundity = $33.68 \cdot (\text{Length} - 1.86)^{1.6}$, $n = 94$, $r^2 = 0.857$. Winter: Fecundity = $15.85 \cdot (\text{Length} - 1.86)^{1.24}$, $n = 56$, $r^2 = 0.512$. The correction term of -1.86 in the allometric equation adjusts for size at first reproduction (Russell, unpublished).

mine brood structure. Although we identified only two seasons with respect to brood number (spring-summer-fall versus winter; Figure 3), the summer-fall broods are very different from the spring broods. Despite having the same levels of brood number, the brood structure differs between the spring and summer-fall samples owing to the variation in the relative proportions of the different sizes of embryos within a brood (Figure 4).

A key feature missing from our analysis of brooding dynamics is information on the relative developmental rates of embryos within a brood. We attempted to measure embryo growth by immersing adults in seawater containing material that would bind to the developing embryonic valves (tetracycline and alizarin red); however, these attempts were unsuccessful. Although no data are available on the turnover rate of embryos within a brood, it appears from the size structure of broods that spring represents the time of year when embryo production is the highest and winter is the period when it is the lowest (Figures 2, 3). During the rest of the year an intermediate rate of reproduction exists. This inference would not be valid if the growth rates of embryos within a brood were slowest in May. This does not seem likely because size structure of the broods changes quickly from the May to the June and July 1987 dissections (Figure 2).

Based on the size structure differences between the broods from the winter and spring samples, we predict that a significant recruitment of juveniles into the adult population should occur sometime in the late winter or early spring. The bulk of the larger embryos that are present in the brood in the winter samples are absent by May (Figure 4). *Transennella confusa* lacks a planktonic stage, and, like *T. tantilla*, has limited dispersal capability (Narchi, 1971; Highsmith, 1985). Therefore, the release of juveniles from the brood would represent a pulse of recruitment into the local adult population. Such a pulse of recruitment was documented for a population of *T. tantilla* at False Bay in May of 1964 (Pamatmat, 1966; Figure 5).

Pamatmat (1966) documented the dynamics of the adult population size structure of *Transennella tantilla* in False Bay from January to September of 1964. From January through April there were no appreciable modes in the size structure of this species; in addition, overall densities were low and there was a noticeable absence of the smaller size classes in the March and April samples (Figure 5). In the May sample Pamatmat found over 100 animals/0.1 m^2 in the <1-mm size class, whereas up until that time no adult size class had more than 10 animals/0.1 m^2. The growth of these individuals from this pulse of recruitment could be tracked in subsequent size-frequency histograms because the mode they represented dominated the adult size structure in the rest of the samples. Lower levels of recruitment continued through the summer and did not di-

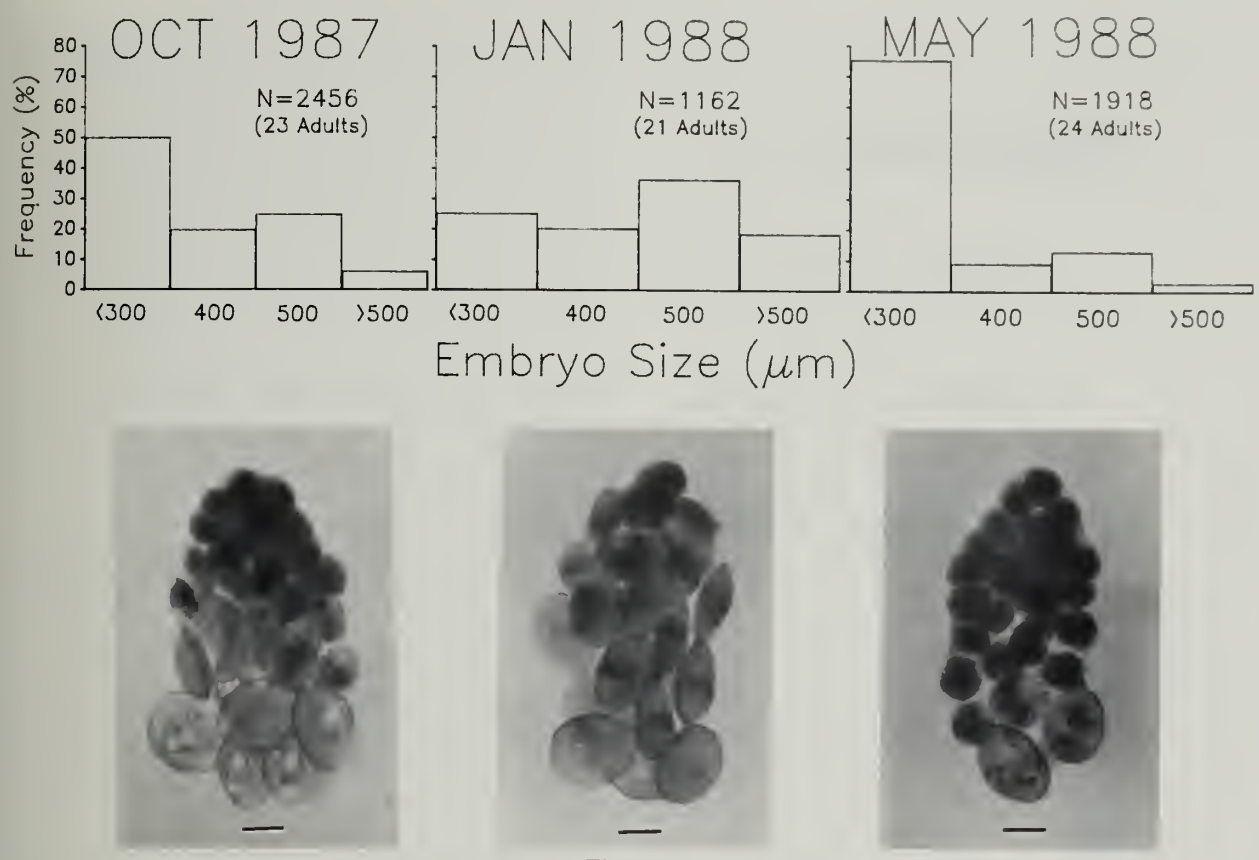

Figure 4

Size-frequency distributions of *Transennella confusa* and accompanying photographs of typical broods from three dissections representing the three kinds of brood structures found in this study. Scale bars are 250 μm.

minish until September (Figure 5). Although the major recruitment episode became evident in the May sample, it is likely that the release of juveniles actually occurred earlier. Newly released juveniles (approximately 600–730 μm long) are small enough to pass through the 500-μm sieve used by PAMATMAT (1966) because the smallest diameter of a bivalve determines whether or not it is retained on a sieve. Therefore, a time lag exists between the actual release of juveniles and when they attain a size large enough to be retained on a 500-μm sieve.

We dissected two samples of *Transennella tantilla* from False Bay, one in August of 1987 and the other in February of 1988. The pattern of seasonal brood structure variation we observed in *T. confusa* at Pillar Point is also apparently occurring in *T. tantilla* at False Bay (Figure 2). Approximately 50% of the August broods are in the <300-μm size class whereas the winter broods are dominated by the larger size classes of embryos. If the two species at the different sites are behaving in a similar manner with respect to brood structure dynamics, then it is reasonable to predict a comparable pattern in the adult population structure. These observations are consistent with our prediction relating the seasonal variation in brood structure to the adult population dynamics.

One explanation for the observed seasonal variation in brood structure relates "aging" of the adult population to brood size structure. This hypothesis predicts that brood size structure reflects the adult population as it "ages" from the spring through the winter; *i.e.*, young adults in the spring tend to brood mostly small embryos whereas old adults in the winter brood mostly larger embryos. If this is in fact occurring, then the spring samples should consist of brooding adults that are smaller than the brooding adults from the winter samples (assuming that adult age is correlated with size). We found no significant difference among season with respect to the sizes of nonparasitized brooding adults in our samples (spring $n = 80$; summer $n = 94$; fall $n = 63$; winter $n = 56$; $P > 0.40$, ANOVA). This clearly falsifies the hypothesis relating seasonal variation in brood structure to growth in the adult population.

Spawning seems to decrease in the winter (Figure 2). Whatever embryos remain in the clutch continue to develop until the brood size structure is composed primarily of the later stages of development (Figure 4). Before spawning increases to the higher spring levels, the brood chamber is emptied of most of the later stages. This "spring cleaning" of the brood chamber should result in an influx of new

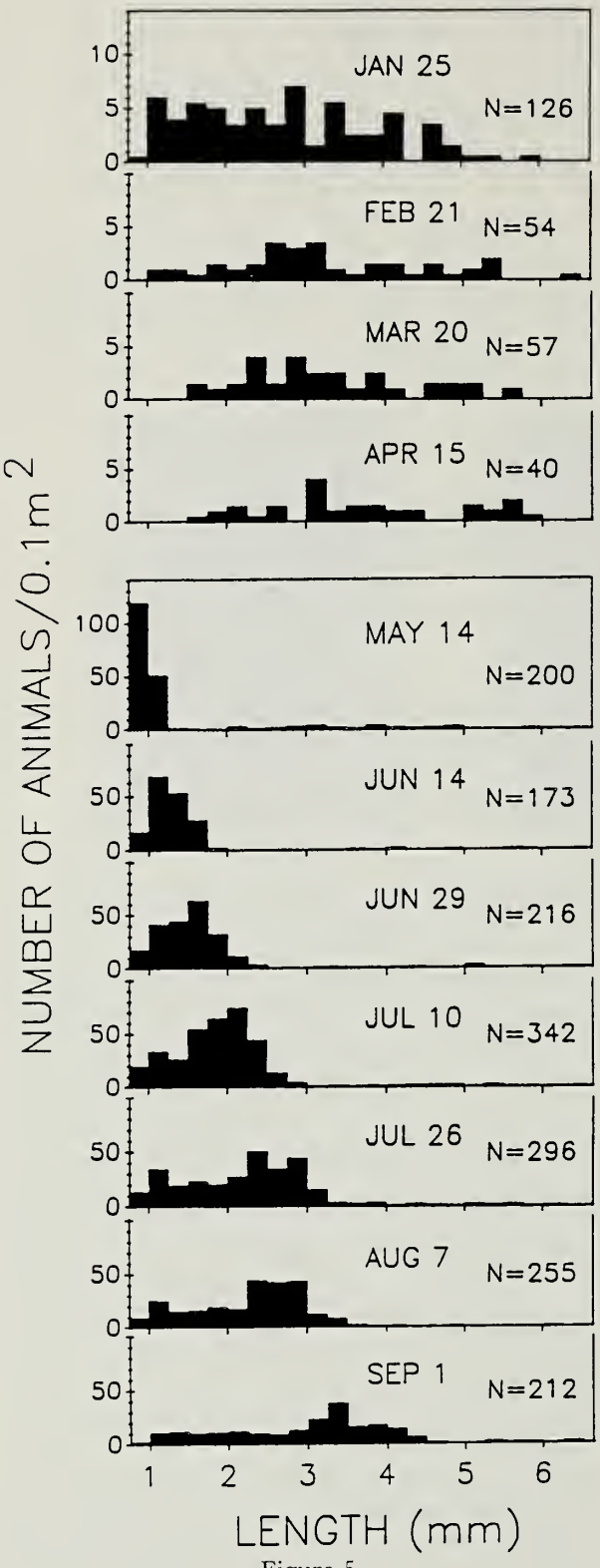

Figure 5

Size-frequency distribution of *Transennella tantilla* from False Bay in 1964. Note that the scale of the ordinate axis for May through September is an order of magnitude greater than the scale for January through April. The spring pulse of recruitment is apparent in the May sample and this cohort influences the shape of the subsequent distributions. Re-drawn from PAMATMAT (1966:147).

individuals into the adult population. Based on the fairly constant proportion of embryos in the <300-μm size class (Figure 2), lower levels of recruitment probably continue throughout the summer and fall. Sometime in the late fall or early winter, when spawning decreases, recruitment most likely also falls. However, recruitment possibly occurs whenever later developmental stages are present in the brood chamber. A similar pattern of reproduction was reported by SELLMER (1967) for the synchronous brooding venerid bivalve *Gemma gemma*. He classified the developmental stage of embryos into three categories: pre-shell, partial shell, and full shell. The highest levels of the pre-shell stage were found in the June-July sample and no pre-shell stages were found in the December-January samples. The highest levels of the full shell stages were found in the December-January samples (fig. 33 and table 5 in SELLMER, 1967).

In summary, *Transennella confusa* displays seasonal variation in brood structure; both brood number and the relative proportions of the different size classes of embryos vary. Fecundity levels are lowest in the winter and this is the time of year that the largest embryos dominate the clutch size structure. Although the levels of brood number are the same throughout the spring, summer, and fall, approximately 75% of the spring brood is in the <300-μm size class, whereas this size class makes up 50% of the summer and fall broods. These brood dynamics combined with observations of the adult population structure of *T. tantilla* at False Bay generate predictions about recruitment events for *T. confusa* at Pillar Point Harbor. Finally, when documenting seasonal reproductive patterns for a brooding taxon it is necessary to consider brood size structure as well as brood number.

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The Malacological Papers and Taxa of Martha Burton Woodhead Williamson, 1843–1922, and the Isaac Lea Chapter of the Agassiz Association

by

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Abstract. Martha Burton Woodhead Williamson, a turn-of-the-century amateur malacologist in southern California, was the author of several significant papers in malacology and marine biology and introduced 11 new names for mollusks. Ten of these names are available; one is a *nomen nudum*. Only two are currently regarded as being valid; the others are synonyms. Type material has been located in the Los Angeles County Museum of Natural History for all but one of the available taxa. Williamson was secretary of the Isaac Lea Conchological Chapter of the Agassiz Association from 1893 to 1898. This small group, founded in 1888, appears to have been America's first independent malacological organization.

INTRODUCTION

Martha Burton Woodhead was born in Rothwell, near Leeds, Yorkshire, England, 6 March 1843, the daughter of Thomas and Virginia Burton Woodhead.[1] Her family moved to Cincinnati, Ohio, in spring 1844, where she attended public school. Her family then moved to Iowa, where she attended Miss Fish's private school, Elliot Seminary, and finally Burlington College, where she had a particular emphasis on philosophy.

During the Civil War, she served on a Christian Commission in Memphis, Tennessee. In 1882, she became associate editor of the Terre Haute, Indiana, *Enterprise*. She married Charles Wesley Williamson, a Civil War veteran, and they had three daughters.

When she and her family moved to Los Angeles in 1887, she became fascinated with marine life. She attended a class at the University of California Marine Biological Laboratory at San Pedro in 1902 and studied biology at the University of Southern California in 1904.

She had a variety of interests and was active in a number of organizations, including the Women's Christian Temperance Union, the University Ethical Club, and the Historical Society of Southern California. She was vice president of the latter for 20 years, writing a number of articles for its publication. Williamson was also the second president of the Southern California Press Club. She wrote many articles on a variety of subjects in a number of magazines, including several in the Sunday *Illustrated Magazine* of the *Los Angeles Times*. Some of her popular articles were published under at least four pen names, particularly "Virginia Burton," and one of her mollusk articles was by "Martha Burton" (WILLIAMSON, 1890a). (I have not attempted to track down all of her popular newspaper and magazine articles on shells, but I have listed those I encountered among archival materials.)

She died on 18 March 1922, at the age of 79. She was described as having been "petite, graceful and scholarly" (Figures 1, 2).

Mrs. Williamson wrote many papers on mollusks and marine biology, most in *The Nautilus*. Particularly significant was a list of the mollusks of San Pedro (WILLIAMSON, 1892b), which contained descriptions of two new taxa by

[1] The information about Williamson's life was obtained from ANONYMOUS (1922), the other newspaper articles mentioned with it in the Literature Cited, and from a holographic autobiography by Williamson in the S. S. Berry archives at the Santa Barbara Museum of Natural History. Some correspondence to her is housed in the Special Collections and University Archives at Stanford University (KEEN, 1982).

Figure 1

Martha Burton Williamson (from BROWN, 1894).

W. H. Dall, the first published figures of a number of Californian species, the introduction of six new names of her own, and notes based on correspondence from J. G. Cooper, C. T. Simpson, and R. E. C. Stearns. Other important papers included several on California abalones (WILLIAMSON, 1894g, 1906b, 1907, 1908), an anatomical monograph on "*Pecten aquisulcatus*" (WILLIAMSON, 1902b), and a discussion of the West Coast Mitridae (WILLIAMSON, 1906c).

She introduced 11 new names for mollusks. One is a *nomen nudum*; the rest are available. Type material has been isolated in the Los Angeles County Museum of Natural History, repository of her collection, for 10 of the available taxa. Only two of these taxa are currently regarded as being valid, both species of *Crepidula*.

The first national organization in the United States devoted to the study of mollusks appears to have been in the Isaac Lea Chapter of the Agassiz Association. The Agassiz Association, founded in 1875, was a popular natural history organization in the 1880s and 1890s. The history of its Isaac Lea Chapter is discussed by WILLIAMSON (1894e).

Walter Harrison of Fisher's Island, New York, an Agassiz Association member, decided in early 1887 that a nationwide malacological society was needed. He wrote to Harlan H. Ballard, Agassiz Association president, who gave him encouragement. Later that year, Dr. M. L. Leach of Michigan had a similar idea and wrote to Harrison.

Figure 2

Martha Burton Williamson (after ANONYMOUS, 1922).

The result was that on 8 February 1888, Ballard certified the Isaac Lea Chapter of the Agassiz Association, to be a national correspondence group devoted to malacology, with Leach as its president and Harrison as secretary, and two other members. Several more joined in 1888 and 1889. Thus, this group predates the American Association of Conchologists (1890–1892) by two years (concerning the latter, see KEEN, 1982, and ABBOTT, 1987:xii–xiii), and its existence was discussed in *The Nautilus* at the time the American Association was started (LEACH, 1890; see also LEACH, 1894). The chapter never reached the 181 members of the Association, but it survived much longer (1888–1899).

Reports were required from each member at least once a year, and these were bound together in manuscript "Transactions," but lack of funds prevented their publication. Instead, papers and the annual Transactions were circulated by mail, from member to member.

By 1893, Josiah Keep was president,[2] and Williamson was secretary, a position she retained until 1898. The group, now called the Isaac Lea Conchological Chapter, was divided into sections—for example, fossil shells and marine shells of the east coast—each with its own section secretary. There were 26 members, including nine juveniles. Dues were 50 cents a year (25 cents for children). Wrote Williamson, "From the Atlantic to the Pacific oceans and in Canada our members are collecting and studying land, fresh-water and marine Mollusca" (Williamson, 1894e).

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[2] Four papers by Keep were unearthed in the course of study that were not in my bibliography for him (COAN, 1985). These were KEEP & WILLIAMSON (1895), listed in the Literature Cited, plus the following:

1893a. The Museum of Amherst College. . . . *In:* WILLIAMSON (1893g).

1893b. Conchological notes. *In:* WILLIAMSON (1893i).

1895. How I became a conchologist. The Observer 6(4):63–64 (April).

On 28 July 1893, the organization held its first meeting, this in Los Angeles, California (WILLIAMSON, 1893f).

From 1893 to 1898, periodic reports of the Isaac Lea Conchological Chapter were published sequentially in three different periodicals, with Williamson as their editor. The five five appeared in *Popular Science News* (WILLIAMSON, 1893d–g, i). The reports then appeared in *The Observer,* journal of the Agassiz Association (WILLIAMSON, 1894a, c, e, f, h; KEEP & WILLIAMSON, 1895). Finally, the reports moved to *The Nautilus* (WILLIAMSON, 1895a–e, 1896a–l, 1897a–h, 1898a). (Most of these last reports edited by Williamson have no original material by her and are entirely excerpts from papers from the 'Transactions.')

By 1895, the chapter claimed 40 members, including 16 juveniles. Reports from members were still bound into a manuscript volume: "The annual reports of the members for the year 1894 form Volume VI of "The Transactions" of the chapter. The vol. is unusually interesting, and many papers are of scientific value. Photographs and water colors add to the beauty of the book, and it is to be regretted that we cannot have the transactions published" (KEEP & WILLIAMSON, 1895).

In January 1898, Dr. William S. Strode took over as general secretary, and a few reports appeared in *The Nautilus* (STRODE, 1898, 1899a–d). After the last of these, the organization seems to have slipped quietly from the malacological scene. In contrast, the Wilson Ornithological Society began in 1888 as a chapter of the Agassiz Association, becoming independent in 1902.

LIST OF TAXA

The following list includes the taxa that Williamson introduced. Each original combination is followed by the original reference (keyed to the Literature Cited). This is followed by type locality, information about type material, and remarks about current allocation. The Literature Cited provides references for Williamson's taxa and any senior homonyms of these taxa, but not for their senior or junior synonyms; references for papers on mollusks and marine biology not containing new taxa are also included.

alba, Olivella biplicata var.—WILLIAMSON, 1892b:212 [*nomen nudum*; *non Oliva alba* MARRAT, 1871:32; pl. 22, fig. 390, an *Olivella*].
San Pedro, Los Angeles Co., Calif.
Remarks: Synonym of *Olivella biplicata* (Sowerby, 1825), according to BURCH (1959:19).

brunnea, Olivella biplicata var.—WILLIAMSON, 1892b:212.
San Pedro, Los Angeles Co., Calif.
Type material: not located.
Remarks: Synonym of *Olivella biplicata* (Sowerby, 1825), according to BURCH (1959:19).

elongata, Nassa mendica var.—WILLIAMSON, 1892b:213, *ex* Stearns MS; WILLIAMSON, 1905b:123 [*non Nassarius elongatus* (SOWERBY, 1815:15–16; pl. 110, fig. 1)].
Santa Catalina Id., Los Angeles Co., Calif.
Type material: LACM 2207, syntypes (16).
Remarks: Synonym of *Nassarius mendicus* (Gould, 1850). Her initial description, though meager, is sufficient to make the name available, in spite of her statement to the contrary in 1905. Her second account suggests that there may have been only one original specimen, in which case additional material was later added to the type lot.

maculata, Drillia moesta var.—WILLIAMSON, 1905b:122–123.
Pt. Fermin, Los Angeles Co., Calif.; 3 specimens, only one of which was retained in her collection.
Type material: LACM 1052, lectotype (SPHON, 1971: 19).
Remarks: Synonym of *Pseudomelatoma penicillata* (Carpenter, 1864), according to KEEN (1971:690).

naticarum, Crepidula rugosa var.—WILLIAMSON, 1905a:50; WILLIAMSON, 1905b:127.
San Pedro, Los Angeles Co., Calif.; at least 4 specimens, one on a piece of *Polinices lewisii* (Gould, 1847).
Type material: LACM 1026, syntypes (2).
Remarks: *Crepidula naticarum* Williamson, 1905, according to HOAGLAND (1977:383, 387; fig. 18), who considered it an older name for *Crepidula coei* Berry, 1950.

norrisiarum, Crepidula rugosa var.—WILLIAMSON, 1905a: 51; WILLIAMSON, 1905b:127 [misspelled as "*morrisiarum*"].
San Pedro, Los Angeles Co., Calif.; on *Norrisia norrisi* (Sowerby, 1838).
Type material: LACM 1027, syntypes (4).
Remarks: *Crepidula norrisiarum* Williamson, 1905, according to HOAGLAND (1977:383–384, 387; fig. 17).

parvum, Calliostoma canaliculatum var.—Williamson, 1905b:128.
San Diego Bay, San Diego Co., Calif.; F. W. Kelsey.
Type material: LACM 2206, syntypes (10).
Remarks: Synonym of *C. canaliculatum* (Lightfoot, 1786).

purpureus, Heterodonax bimaculatus var.—Williamson, 1892b:187.
San Pedro, Los Angeles Co., Calif.
Type material: LACM 1168, lectotype (COAN, 1973: 46; fig. 12); LACM 1176, paralectotypes (8 pairs, 2 valves).
Remarks: Synonym of *H. pacificus* (Conrad, 1837) (COAN, 1973).

rosea, Corbula luteola var.—WILLIAMSON, 1905b:120 [*non* REEVE, 1844:pl. 4, fig. 26].
Terminal Id., San Pedro, Calif.; valve on a sea anemone in a rock pool on the old breakwater.
Type material: LACM 1421, syntypes, 2 valves.
Remarks: Synonym of *C. luteola* Carpenter, 1864, according to BERNARD (1983:58). Apparently, a second valve was added to the type lot at a later date.

salmoneus, Heterodonax bimaculatus var.—Williamson, 1892b:187.

San Pedro, Los Angeles Co., Calif.

Type material: LACM 1169, lectotype (Coan, 1973: 47; fig. 13); LACM 1177, paralectotypes (1 pair, 21 valves).

Remarks: Synonym of *H. pacificus* (Conrad, 1837) (Coan, 1973).

splendidula, Haliotis cracherodii var.—Williamson, 1892b: 198; Williamson, 1905b:128–129.

Pt. Vicente, Los Angeles Co., Calif.; a number of specimens; 1890.

Type material: LACM 1035, lectotype (Sphon, 1971: 12).

Remarks: Synonym of *H. cracherodii* Leach, 1814, according to Abbott (1974:17). The name was made available in 1892; in 1905, she indicated that it had been *ex* Dall MS.

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A New *Elysia* (Opisthobranchia: Ascoglossa) from the Florida Keys

by

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Abstract. *Elysia* ***cornigera*** sp. nov. from the southern Florida Keys is described. This species is found in sheltered, shallow water, feeding on *Acetabularia crenulata*. It lays between 77 and 137 eggs in a colorless spiral mass on the corona superior of *A. crenulata*. In appearance, *E.* ***cornigera*** is small and warty; the body is white to olive green, with small brilliant red and pale orange granular spots, as well as bright green intestinal diverticula, visible through the colorless epidermis. The animal has large warty rhinophores that are swept forward, resembling horns. The teeth of *E.* ***cornigera*** are long and narrow, tri-keeled, bi-serrated, and up to 216 μm long.

INTRODUCTION

Ten species of *Elysia* are currently known from Florida (Jensen & Clark, 1983; Marcus, 1980). Most feed on green siphonalean algae in relatively shallow water. A few specimens of a suspected new species were collected by Joyce G. Nuttall in very shallow water on the Florida Bay side of Long Key on 23 July 1986. These animals were associated with *Acetabularia crenulata* Lamouroux, an alga until now with no known Floridian ascoglossan predator. Based on morphology, dentition, developmental data, and ecological data, I propose the following taxon:

Family Elysiidae

Genus *Elysia* Risso, 1818

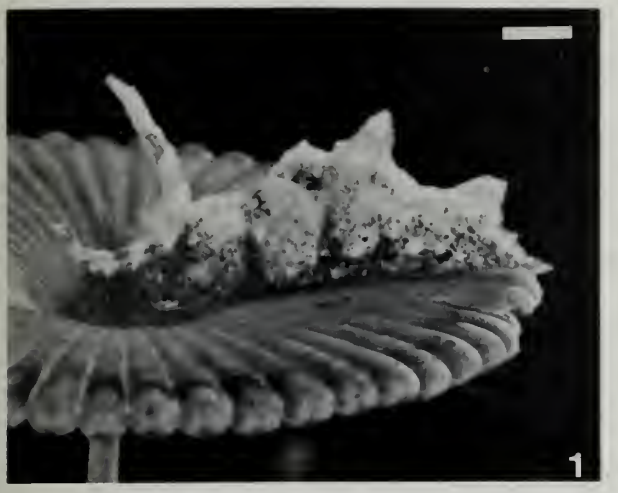
Elysia ***cornigera*** Nuttall, sp. nov.

Type material: The holotype (USNM 859144) and five paratypes (USNM 859145) from West Summerland Key have been deposited at the National Museum of Natural History, Smithsonian Institution.

Type locality and distribution: Following the initial collection of five animals at Long Key, 26 specimens were collected at the southwestern end of West Summerland Key (24°39.7'N, 81°18.1'W). *Elysia* ***cornigera*** has been found only on the Florida Bay side of Long Key, West Summerland Key, and Sugarloaf Key. The type locality is Spanish Harbor at West Summerland Key on and around *Acetabularia crenulata* in very shallow, sheltered water on hard substrata (rock or sand over rock).

Diagnosis: Species small (to 8 mm); very warty; general white to olive green appearance with brilliant red and pale orange spots over most of the body; epidermis transparent and colorless; bright green diverticula evident, especially between parapodia; one or two pairs of dorsal parapodial extensions; rhinophores robust at base but tapering to a smooth point, often held in forward position resembling bull's horns; penis bent, below right eye, up to 1 mm long, and unarmed; renopericardium short, with two major dorsal vessels connecting posterolaterally, then branching both anteriorly and posteriorly; teeth slender, tri-keeled, and bi-serrated, to 216 μm long; head large, in small specimens up to 40% of total body length (Figures 1, 2).

Description: Although with the unaided eye *Elysia* ***cornigera*** appears to be dirty white, with a lens many bright colors can be seen (Figure 3). The outer epidermis is clear and colorless, with all the animal's color originating from deeper structures. The white appearance is due to small, white granules 15 μm in diameter that cover the entire animal. Additionally, larger white granules 46 μm in diameter are grouped in small clusters around blind ducts along the base of the parapodia. Brilliant green intestinal diverticula enter all parts of the body, including the head and rhinophores, and are occasionally seen through the transparent epidermis between the small, white granules. These diverticula, each about 30 μm across, branch off larger main ducts. Red granules, 45 μm in diameter, are located just below the epidermal surface and, although found over most of the body, are usually concentrated on the head, rhinophores, and outer surface of the parapodia.



Explanation of Figures 1 and 2

Figure 1. *Elysia cornigera* sp. nov. (lateral view) on *Acetabularia crenulata* showing hornlike appearance of rhinophores and parapodial extensions. Bar = 1 mm.

Figure 2. *E. cornigera* (dorsal view). Note slender, forward-swept tips of the rhinophores and general warty appearance. Inset: Inrollment of the rhinophores (ventrolateral view). Bar = 1 mm.

These red spots vary in number from zero to nearly a hundred per animal, with a dozen or two being common. Pale translucent orange vesicles lie somewhat deeper under the epidermis than the red spots and are always larger, up to 80 μm in diameter. These orange spots are restricted to the outer surface of the parapodia and the sides of the foot. The orange and red spots are not associated with vessels or other structures. Finally, around the oral lobes are small, black spots that create a typical elysiid "mustache," as in *E. subornata* Verrill, 1901.

The renopericardium is short, with two main vessels leaving laterally and proceeding lateroposteriorly (Figure 4). Between the dorsal vessels, at the base of the parapodia, lie many yellowish glands. From a previously frozen specimen, these glands are ovoid, about 540 μm long, and yellow-cream colored on one end, while the other end is more colorless. A duct, attached to the colorless end, travels a short distance and is surrounded by a cluster of smaller (80 μm), colorless saclike vessels. Under high magnification, these small, colorless vessels appeared to contain sperm: thus the entire structure is part of an ovotestis network. The mucous gland is behind and to the right of the head, and in a thawed specimen, the gland swelled with water to distort the entire animal.

Egg masses, about 2 mm in diameter, are laid on either the upper or lower surface of the cup (corona superior) of *Acetabularia crenulata*. Each egg spiral contains from 77 to 137 eggs. Capsule size and volume and egg size are given in Table 1. When first deposited, the capsular cytoplasm is opaque, but clears within 10 to 15 min. An extra-capsular ribbon of clear, colorless, refractile yolk winds around the egg case. The uncleaved egg is about 105 μm in diameter (Table 1). The embryo grows to 225 μm in length in the encapsulated veliger stage. The veliger shell possesses a distinct extension at the aperture (Figure 5). Unfortunately, as the veligers began resorbing the velar lobes the egg mass died. No animals were seen hatching, but Type 2 or 3 (metamorphic) (Bonar, 1978) development is predicted.

Figure 3

Camera lucida drawing showing color distribution. Solitary black spots = red spots; outlined spots = orange spots; stipling = green diverticula. Remainder of animal is white. Bar = 1 mm.

Figure 4

Camera lucida drawing of an animal with parapodia held open with a round coverslip. Renopericardium (a) and visible portions of ovotestis (b) are shown. Bar = 1 mm.

Table 1

Character comparison between *Elysia* ***cornigera*** sp. nov. and *E. timida*. A = Clark & Jensen, 1981; B = Bouchet, 1984; C = Thompson & Jaklin, 1988; D = Ros & Rodriguez, 1985; "?" = cannot determine from available information.

	E. cornigera	*E. timida*	References
Egg diameter (μm)	105	120	A
Egg volume (mm^3)	61×10^{-5}	90×10^{-5}	A
Capsule dimensions (μm)	291 × 268	300 × 200	A
Capsule volume (mm^3)	1097×10^{-5}	626×10^{-5}	A
Appearance	warty	smooth	B, C, D
Rhinophore shape	pointed	blunt	B, C, D
Orange spots	present	absent	B, D
Red spots	small	large	B, C, D
Teeth	tri-keeled, bi-serrated	? ?	

Explanation of Figures 7 and 8

Figure 7. Lateral view of tooth of *Elysia* ***cornigera*** showing serrated keel. Bar = 10 μm.

Figure 8. Lateral view of tooth of *E.* ***cornigera*** showing non-serrated keel. Bar = 10 μm.

←

Explanation of Figures 5 and 6

Figure 5. Veliger shell of *Elysia* ***cornigera***. Bar = 20 μm.

Figure 6. Radular tooth of *E.* ***cornigera*** showing the tri-keeled, bi-serrated, cutting surface. Bar = 2 μm.

The buccal mass contains 2–5 ascending and 6 or 7 descending teeth, with over a dozen juvenile teeth heaped in the ascus. Teeth are long and narrow, typically 117–160 μm long (but up to 216 μm), with a tri-keeled, bi-serrated cutting edge (Figure 6). The serrated lateral keel is long and contains denticles that point forward (Figure 7). The unserrated lateral keel is short and smooth (Figure 8). Between the cutting edges the surface is deeply concave (Figure 6). The dorsal notch is broad to accommodate the preceding tooth.

Ecology: *Elysia* ***cornigera*** is closely associated with *Acetabularia crenulata,* which grows mainly in very shallow (<40 cm) water. Many animals were collected crawling over stones containing filamentous green algae up to 4 m from the nearest macroalgae. As the standing crop of *A. crenulata* was declining (compared to previous months), *E.* ***cornigera*** may have been exploiting other food sources.

Elysia ***cornigera*** feeds upon *Acetabularia crenulata* by puncturing utricles one or two at a time and sucking the sap out. Although no detailed observations of feeding behavior were made on this alga (because the mouth was typically obscured by the animal itself or by the alga), radular puncture marks were seen on utricles recently fed on. One animal was observed feeding on a small, filamentous alga. The animal moved slowly, maintaining a hunched appearance as it examined the alga with its oral lobes, pierced the alga with its leading radular tooth, and quickly sucked the contents out. Fecal material was ejected from the anus simultaneously with the pumping of algal sap into the buccal mass. This phenomenon was also observed while *Ercolania fuscata* (Gould, 1870) was feeding on *Bryopsis plumosa* (Hudson) C. Agardh—a steady stream of fecal egesta was released as long as feeding continued. When feeding stopped, only an occasional fecal pellet was released.

Etymology: The specific name is taken from the Latin *corniger* meaning "horned."

DISCUSSION

Elysia ***cornigera*** can easily be distinguished from all western Atlantic elysiids by its unique teeth, general appearance, and ecological habitat. The best external characters for species identification are warty, tapering rhinophores, red and orange spots, colorless epidermis containing white granules, and parapodial extensions. This species occurs in warm, shallow water and feeds on *Acetabularia* sp. No other *Elysia* sp. in the Caribbean has been found in this habitat.

Some physical and ecological characteristics of *Elysia* ***cornigera,*** while unique in the Caribbean Sea, are found in elysiids from other parts of the world. In Guam *E. mercieri* (Pruvot-Fol, 1930) (Carlson & Hoff, 1978) has similar long, warty, pointed rhinophores, white dots covering the body, and projections above the parapodial margin. Although these parapodial projections are branched and represent true projections rather than just extensions of the parapodial margin, they occur in precisely the same locations as the pointed parapodial extensions of *E.* ***cornigera***.

The closest apparent relative of *Elysia* ***cornigera***, *E. timida* Risso, 1818, occurs in the Mediterranean Sea. *Elysia timida* is similar to *E.* ***cornigera*** in coloration, rhinophore shape, dorsal venation, parapodial shape, and diet (Swennen, 1961; Ballesteros, 1979; Schmekel & Portman, 1982—see fig. 7.94, which is mistakenly labelled *E. viridis* (Montagu, 1804), but is actually *E. timida* [Bouchet, 1984]; Ros & Rodriguez, 1985; Thompson & Jaklin, 1988). However, several important characters of *E.* ***cornigera*** are absent in *E. timida,* such as epidermal warts, orange spots, parapodial extensions, and a tri-keeled, bi-serrated tooth (Table 1).

The leading tooth of *Elysia* ***cornigera*** is less delicate than the tooth of *E. timida* pictured by Bouchet (1984). The tip of the leading tooth of *E.* ***cornigera*** is pointed like that of *E. timida* (Bouchet, 1984), but older teeth in the descending radula are blunt-tipped, as drawn by Swennen (1961). The base of the tooth in *E.* ***cornigera*** is squared, as that of *E. timida* pictured by Swennen (1961) rather than pointed (Bouchet, 1984). Other similar characteristics may be found when the three-dimensional structure of more elysiid radular teeth is investigated by scanning electron microscopy. Lateral views of radulae seen in slide mounts often obscure this particular aspect of the teeth. It is easy to understand how the teeth of *E. timida* pictured by Swennen (1961), Bouchet (1984), and Thompson & Jaklin (1988) can look so different.

Similarities between *Elysia* ***cornigera*** and *E. timida,* such as morphology and diet, suggest that these species may be evolutionarily close. A genetic comparison between these species, as well as among other Atlantic ascoglossan species, would help estimate evolutionary relationships in the Atlantic Ascoglossa. Among Caribbean ascoglossan species, electrophoretic techniques show large genetic distances between species and reveal unsuspected sibling species. *Elysia* ***cornigera*** is genetically distinct from other Caribbean elysiids; it has a Nei's genetic identity of 0.37 when compared (at 11 loci) with other species in its clade: *E. tuca* Marcus, 1967, *E. papillosa* Verrill, 1901, *E.* sp. (an undescribed species that is morphologically similar to *E. papillosa*), and *E. serca* Marcus, 1955. The genetic dissimilarity is greater when comparing *E.* ***cornigera*** with the other two members in its clade, *E.* (*Tridachia*) *crispata* Morch, 1863, and *E. patina* Marcus, 1980, and to a *subornata* clade containing *E. subornata* and two undescribed species (Nuttall, unpublished data). The Caribbean Sea shares many ascoglossan species with the eastern Atlantic Ocean and the Mediterranean Sea; thus a genetic comparison between amphi-Atlantic populations would indicate whether sibling status is needed for some species.

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A New Species of *Holospira* (Gastropoda: Pulmonata) from Arizona, with the Reproductive Anatomies of *H. arizonensis* and *H. chiricahuana*

by

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Abstract. A new species, *Holospira* ***sherbrookei*** Gilbertson, is described from the Chiricahua Mountains of southeastern Arizona. It is the first *Holospira* von Martens, 1860, exhibiting a quadrilamellate shell to be described from the state and adjacent region. The reproductive anatomies of two nearby species, *H. arizonensis* Stearns, 1890, and *H. chiricahuana* Pilsbry, 1905, are also illustrated and compared.

INTRODUCTION

The Chiricahua and adjoining Dos Cabezas Mountains of southeastern Arizona form a northern extension of the Mexican Sierra Madre Occidental. They are inhabited by three known species of land snails in the genus *Holospira*: *H. arizonensis* Stearns, 1890, *H. chiricahuana* Pilsbry, 1905, and *H. cionella* Pilsbry, 1905 (Pilsbry, 1946:142–151). These, and all other species of *Holospira* from Arizona, New Mexico, and the Guadalupe Mountains of northwestern Texas, appear to form a monophyletic group. They are known on the basis of their shells alone, which are characterized by being short-whorled and unusually variable in regard to several shell features, including the number of internal lamellae (one to three). J. C. Bequaert (Bequaert & Miller, 1973:43, 138) adopted the subgeneric name *Eudistemma* Dall, 1895, for these species, thus removing them from subgenus *Bostricocentrum* Strebel, 1880 (see Pilsbry, 1946:122–123).

This paper describes a fourth species of *Holospira* from the Chiricahua Mountains. Its shell is similar externally to the shells of other species in the subgenus *Eudistemma*. However, its quadrilamellate interior is diagnostically unlike that of all other described species from this southwestern region of the United States.

SYSTEMATICS

Family Urocoptidae

Subfamily Holospirinae

Genus *Holospira* von Martens, 1860

Subgenus *Holospira s.s.* von Martens, 1860

Holospira ***sherbrookei*** Gilbertson, sp. nov.

(Figures 1, 2)

Diagnosis: A medium-sized *Holospira* with a cylindric-turriform, quadrilamellate shell. Its reproductive system is characterized by a long, slender epiphallus that inserts laterally into the penis, and by the presence of a diverticulum on the spermathecal duct.

External morphology: Animal light silvery gray in color and rather transparent. Mantle collar often embedded with many small, elongated, green bodies and numerous smaller white spots. Foot slender, ca. 7.0 mm in length, by ca. 1.0 mm in width.

Description of shell of holotype: Shell medium-sized for genus, cylindric-turret in shape, imperforate, subtrans-

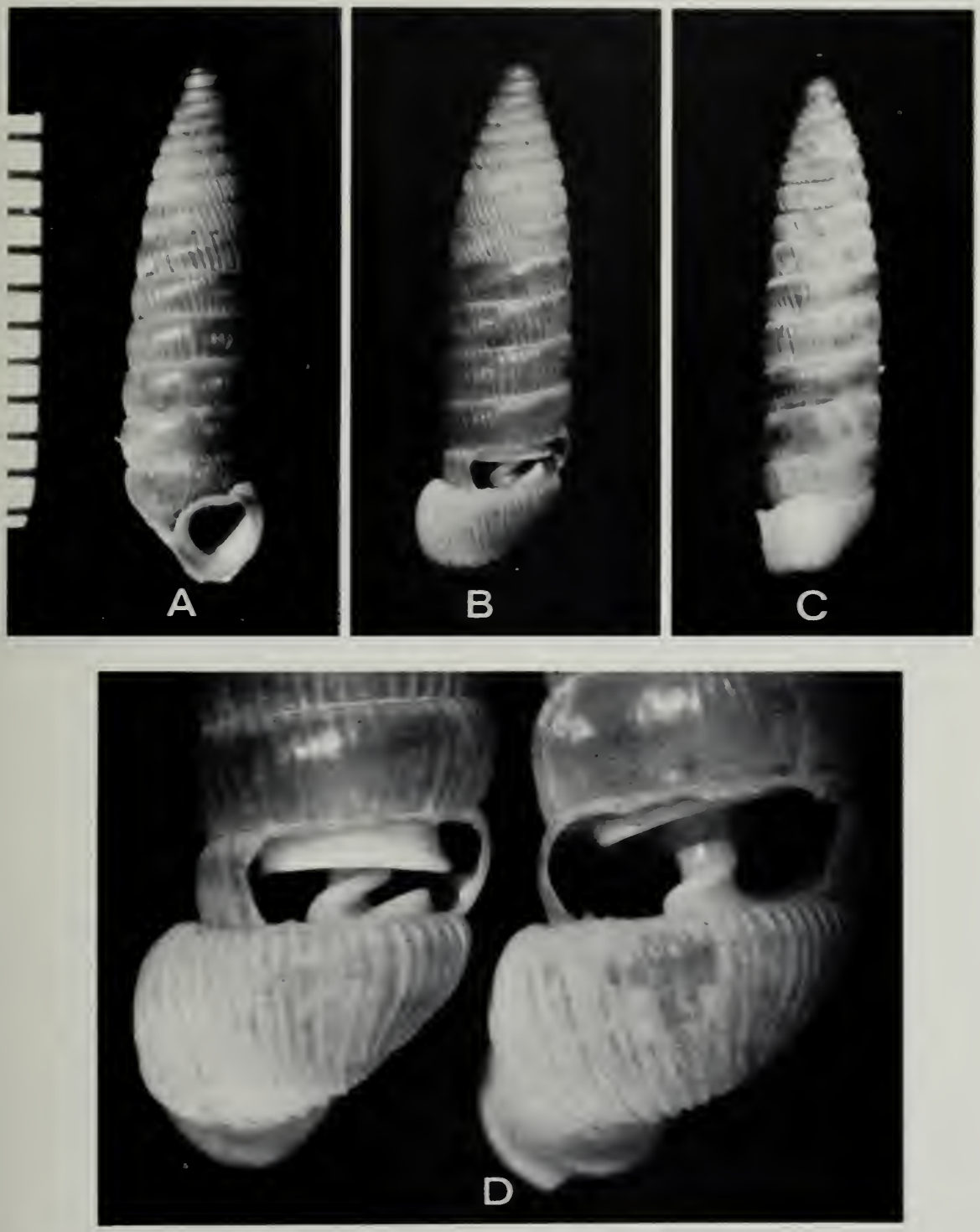

Figure 1

A and B. *Holospira* ***sherbrookei***, sp. nov., holotype, Santa Barbara Museum of Natural History No. 35043, apertural view (A) and dorsal view (B). C. Side view of paratype. D. Enlargement to show internal lamellae of *H.* ***sherbrookei*** holotype (left) and *H. a. arizonensis* (right). Scale in mm.

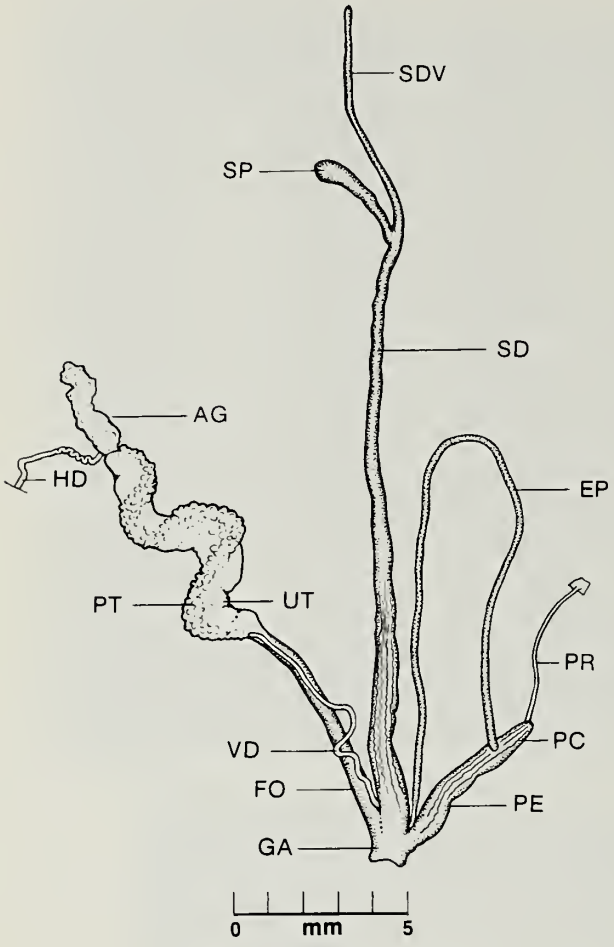

Figure 2

Reproductive system of *Holospira* ***sherbrookei***, sp. nov. Specimen collected at type locality, 16 April 1987. L. H. Gilbertson slide No. 11. Abbreviations: AG, albumen gland; EP, epiphallus; FO, free oviduct; GA, genital atrium; HD, hermaphroditic duct; PC, penial caecum; PE, penis; PR, penial retractor muscle; PT, prostate gland; SD, spermathecal duct; SDV, spermathecal diverticulum; SP, spermatheca; UT, uterus; VD, vas deferens.

parent, composed of 15.0 whorls (Figures 1A, B). Embryonic whorls 2.5 in number, rounded, smooth, tapering toward apex. Apical postembryonic shell, consisting of 7 gradually enlarging convex whorls, tannish in color, sculptured with distinct, oblique, axial ribs separated by intercostal spaces about twice as wide as ribs. Cylindric portion of shell medium brown in color, glossy, with axial ribs becoming vertical and subobsolete. Last half of body whorl opaque white, strongly costate in the region of a thick callus, slanting basally from callus to peristome, compressed laterally, and extending laterally from penultimate whorl. Internal column slender, hollow. Aperture ovate-auriculate; peristome simple and barely extended from body whorl. Armature of four strong lamellae in penultimate whorl (Figure 1D, left). Axial and parietal (superior) lamellae particularly well developed, extending entire length of whorl; basal shorter, extending one-third length of whorl; palatal rather weak but clear, appearing as a white line on side of whorl when viewed externally. Greatest development of lamellae occurring one-third distance from proximal end of penultimate whorl. Shell 14.0 mm in length, 3.8 mm in width.

Table 1

Measurements (mm) of reproductive anatomies figured in this paper.

	Holospira sherbrookei	*Holospira a. arizonensis*	*Holospira c. chiricahuana*
Penis (including caecum)	4.8	2.8	4.7
Epiphallus	20.8	16.3	15.0
Penial retractor	4.2	2.5	2.2
Spermathecal duct	16.8	14.8	10.5
Spermathecal diverticulum	7.0	12.0	5.3
Spermatheca (to junction)	3.2	4.0	2.5
Free oviduct	6.1	3.8	4.0
Uterus	8.5	8.8	6.8

Shell variation: Twelve representative paratypes range from 13.0 to 13.9 mm (mean 13.4 mm) in length, 3.5 to 3.9 mm (mean 3.6 mm) in width, and have 14.0 to 15.2 (mean 14.7) whorls. Several specimens are a more uniform, brown color (except body whorl) compared to holotype. Some exhibit well-developed axial ribs on cylindric portion of shell. Penultimate whorl of 30 remaining shells has been opened to expose lamellae: 27 quadrilamellate, 2 trilamellate (lacking palatal), and 1 unilamellate (reduced axial only).

Description of reproductive anatomy: Reproductive anatomy (Figure 2) generally similar to other described urocoptid anatomies. Penis of moderate size, containing several internal folds, continuing apically as a caecum (see Thompson, 1976). Epiphallus very long and slender, inserting laterally into penis; first third glandular, middle third slightly so. Penial retractor muscle slender, attaching near apex of penial caecum. Spermathecal duct long, rather wide, bearing a diverticulum; basal portion containing several longitudinal internal folds. Spermatheca elongate. Vagina and accessory glands lacking. Free oviduct of average length with slightly convoluted vas deferens alongside it. Retractor muscle (not shown) inserting on basal portions of oviduct and spermathecal duct. Uterus of typical size and shape with attached prostate gland rising from surface. Albumen gland small, elongate. Length measurements of distinctive structures given in Table 1.

Description of radula: Radula typical for genus; formula (14–15)·6·1·6·(14–15). Central and lateral teeth consisting of conic mesocone; first marginal tooth developing a short ectocone which enlarges on ensuing marginals.

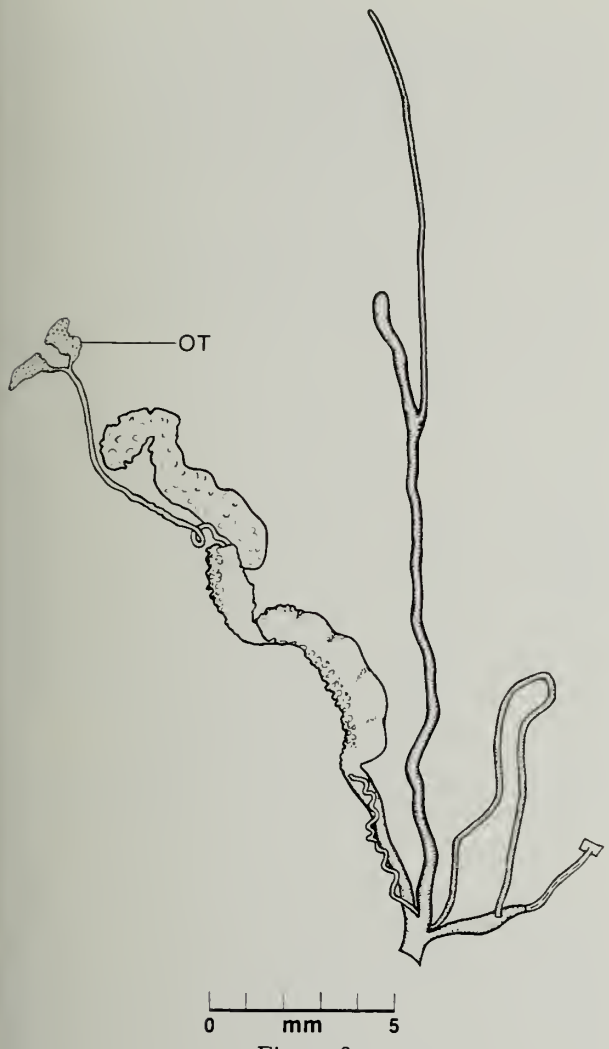

Figure 3

Reproductive anatomy of *Holospira a. arizonensis*. Specimen collected at the Cave at Dos Cabezas, Cochise Co., Arizona (type locality), by W. B. Miller, 30 March 1971. W. B. Miller slide No. 5359. OT, ovotestis.

Mesocone becoming variably bifurcate on marginals ca. 3–11.

Type locality: The type locality is in Silver Creek Canyon of the Chiricahua Mountains, near an unnamed mine, 3.4 road miles (5.7 km) west of Portal along the road to Paradise, Cochise County, Arizona; 31°57.0′N, 109°10.5′W; elevation ca. 1590 m. It is a comparatively hot, south-facing slope in the Upper Sonoran Life-zone with vegetation consisting of scattered bushes, agaves, and cacti. Dominant plant species at the site include *Juniperus monosperma, Dasylerion wheeleri, Agave palmeri, Fouquieria splendens, Acacia greggi, Acacia constricta, Opuntia thaecantha, Rhus microphylla,* and *R. choriophylla*. The hillside is characterized by a fairly extensive limestone outcropping. Specimens were found estivating under rocks.

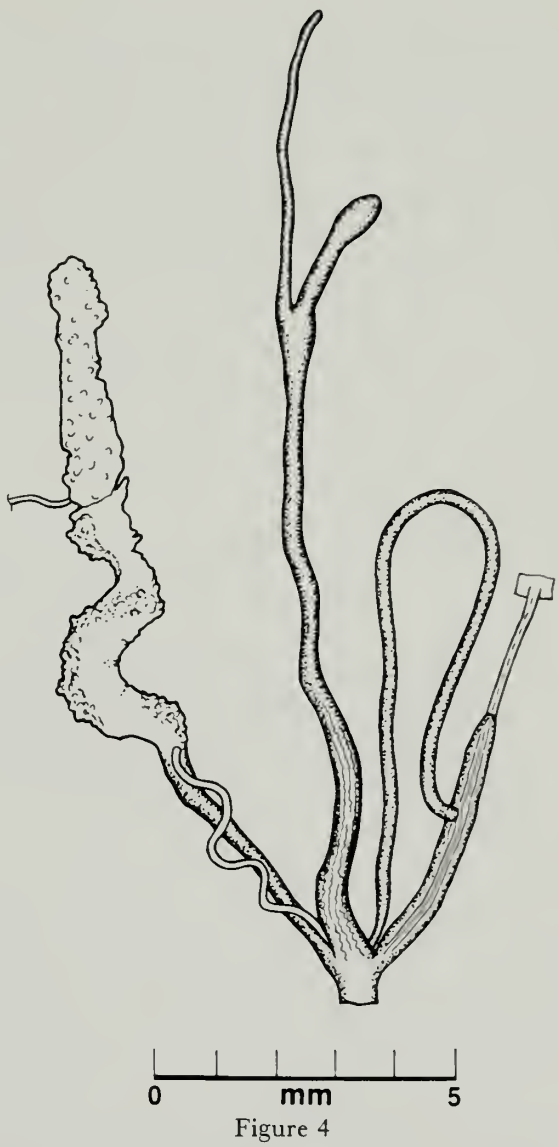

Figure 4

Reproductive anatomy of *Holospira c. chiricahuana*. Specimen collected in Cave Creek Canyon, Cochise Co., Arizona (type locality), 15 April 1987. L. H. Gilbertson slide No. 8.

Etymology: This species is named for Wade C. Sherbrooke, a long-time friend and resident director of the Southwestern Research Station of The American Museum of Natural History located in the Chiricahua Mountains. He was very helpful in the discovery of the new species.

Disposition of types: Holotype: Santa Barbara Museum of Natural History No. 35043. Paratypes: Academy of Natural Sciences of Philadelphia No. 371717; National Museum of Natural History No. 860424; University of Texas at El Paso No. 11107; Field Museum of Natural History No. 208713; Florida Museum of Natural History No. 122794, Los Angeles County Museum of Natural History No. 2209, L. H. Gilbertson No. 66.

Discussion: The subgenus *Holospira s.s.* is defined by the presence of four lamellae within the penultimate whorl of the shell. Based on limited fossil evidence, it is hypothesized that the possession of all four lamellae was the primitive, ancestral *Holospira* condition and that, subsequently, many species have lost some or all of these lamellae (PILSBRY, 1953:140). Accordingly, *H. **sherbrookei*** is thought to retain the primitive lamellar condition and all other known species from Arizona, New Mexico, and northwestern Texas have become reduced and quite variable in this respect.

The shell of *Holospira **sherbrookei*** most resembles that of *H. arizonensis*. However, the shells of *H. a. arizonensis,* and the similar *H. a. emigrans* Pilsbry & Ferriss, 1910, are slightly wider and more cylindric, with a conic apex. Internally, the lamellae are fewer (usually one or two), more variable, and reduced in size compared to those of *H. **sherbrookei*** (Figure 1D).

The reproductive anatomy of *Holospira **sherbrookei*** is generally similar to those of *H. arizonensis* (Figure 3) and *H. chiricahuana* (Figure 4). However, the male genitalia of *H. arizonensis* are smaller, and its spermathecal diverticulum is more slender and substantially longer than that of *H. **sherbrookei***. By comparison, the reproductive tract of *H. chiricahuana* is smaller overall; however, the male genitalia are comparable to those of *H. **sherbrookei***.

In contrast, the reproductive anatomy of *Holospira **sherbrookei*** is quite unlike that of the two other members of the subgenus *Holospira s.s.* for which the anatomy is known. One, *H. goldfussi* (Menke, 1847), from south-central Texas (the only other United States species in this subgenus) lacks a spermathecal diverticulum and exhibits a "capacious" vagina (PILSBRY, 1903:pl. 19, fig. 52). The other species, *H. milleri* Gilbertson, 1989, from adjacent Sonora, Mexico, also lacks a spermathecal diverticulum and contains a verge in its penial complex. It also lacks the long, tubular epiphallus characteristic of *H. **sherbrookei*** (see GILBERTSON, 1989). Hence, based on its reproductive anatomy, *H. **sherbrookei*** appears to be very closely related to species in the subgenus *Eudistemma,* and only distantly to other members of *Holospira s.s.*

The foregoing represents anatomical evidence that *Holospira s.s.* is not a valid phylogenetic group, but rather a "form-subgenus" composed of numerous, diverse species that exhibit quadrilamellate shells. It appears that this subgenus will need revision at some point using characters more dependable than the number of internal lamellae (see PILSBRY, 1953:141).

ACKNOWLEDGMENTS

I wish to express my sincere thanks to Walter B. Miller for sponsoring me at the University of Arizona and for the loan of the slide-mounted reproductive anatomy of *Holospira arizonensis* that is figured, to James E. Hoffman for generous assistance and shared office space at Arizona, to Mary A. Garback at the Philadelphia Academy of Sciences for the loan of holotype and paratype shells of *H. a. emigrans,* to Dwayne L. Moses for the drawings of the reproductive anatomies, to Wade C. Sherbrooke for identifying the plant species at the type locality, to my wife, Nancy, and son, Scott, for aiding me on this and other collecting expeditions, and to the Trustees of the Coast Community College District for the privilege of a sabbatical leave during which time this research was initiated.

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Status of *Penitella gabbii* (Tryon, 1863) in the Eastern and Western Pacific, and Description of the Previously Misidentified Eastern Pacific Species (Bivalvia: Pholadidae)

by

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Abstract. The pholadid bivalve *Penitella gabbii* (Tryon, 1863), originally cited as coming from the "Coast of Japan?" but believed by Tryon to be a California species, has been treated erroneously by all subsequent workers as an eastern Pacific species. The species is actually from the western Pacific and occurs at least from northeastern to southwestern Japan. "*Penitella gabbi (i)*" of authors, not Tryon, 1863, from the Pacific coast of North America, is without an available name and is described herein as *P. **richardsoni*** sp. nov.

INTRODUCTION

Despite several existing monographs on the family Pholadidae (Mollusca: Bivalvia) of the eastern Pacific region (TURNER, 1954, 1955; KNUDSEN, 1961; KENNEDY, 1974), a number of nomenclatural problems in the family remain unresolved (KENNEDY, 1985), particularly among species of *Penitella* Valenciennes, 1846, from the North Pacific region. This paper discusses the status of *Penitella gabbii* (Tryon, 1863) in the eastern and western Pacific, and describes as new the previously misidentified eastern Pacific species.

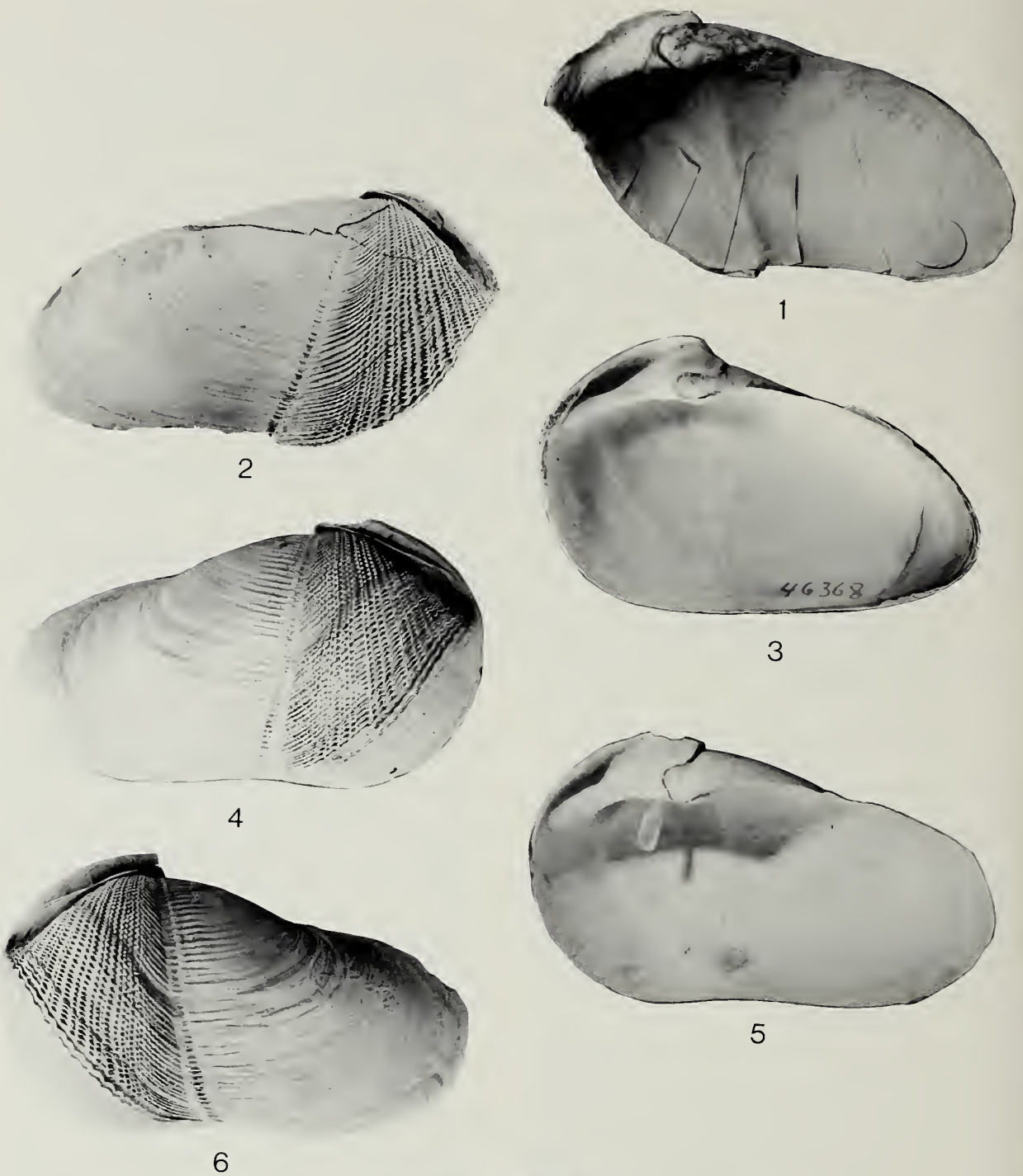
Penitella gabbii was described as *Zirphaea gabbii* Tryon, 1863, and considered by its author to be a Californian species. For nearly 70 years, however, the name was applied to the common eastern Pacific *Zirfaea* by most workers. LOWE (1931:52) recognized that Tryon's species belonged in *Penitella,* but erroneously placed it in synonymy with *P. penita* "var." *concamerata* (Deshayes, 1839), itself a junior synonym of *P. penita* (Conrad, 1837). Although *Zirfaea pilsbryi* Lowe, 1931, was proposed for the eastern Pacific *Zirfaea,* the combination "*Zirfaea gabbi (i)*" continues to creep into the literature.

TURNER (1955) interpreted TRYON's (1863) species to be the *Penitella* that is best known from museum specimens from Monterey Bay, California, a site subsequently designated by her as the "type locality" (TURNER, 1955:87). This interpretation of *P. gabbii* was followed in citing fossil records for the species (KENNEDY, 1974:45-47). Recent examination of the holotype of *Zirphaea gabbii* (=*Penitella gabbii*), and of new and previously unstudied specimens of Japanese pholadids in USA and Japanese collections, suggests that this interpretation was incorrect (KENNEDY, 1985:13).

The description of *Zirphaea gabbii* was based on "a single valve, somewhat mutilated" from the "Coast of Japan?" (TRYON, 1863:44). However, the situation was better explained by GABB (1869:52-53), thusly:

> This shell was described by Mr. Tryon from a single dead valve, sent to him by me from San Francisco. I obtained it from a miscellaneous collection of shells from Japan, and have no reason to doubt but that the specimen came from Japan with the collection. Mr. Tryon has long held the belief that it was mixed with the others by accident, and that it was a California specimen. However that may be, I cannot tell; and we have, at present, no means of settling the question. The species is found in California in both a recent and fossil state, large valves [=*Zirfaea pilsbryi*] being quite common in the Post-Pliocene [=Pleistocene] of San Pedro; nevertheless I do not consider this any proof that it may not, likewise, be found living in Japan.

Despite these early comments about a possible Japanese origin for the type specimen, no subsequent worker has compared it with other Japanese specimens. Examination



Explanation of Figures 1 to 6

Figures 1–6. *Penitella gabbii* (Tryon, 1863). Figures 1, 2: ANSP 51085, holotype of *Zirphaea gabbii,* from "Coast of Japan?"; length, 56 mm. Specimen is adult shell with most of callum broken away. Figure 3: CAS 028806 (*ex* SU 46368), from Onahama Bay, Fukushima Pref., Japan; length, 49 mm. Figures 4–6: USNM 563670, from Yotsukura coast, Fukushima Pref., Japan; length, 60 mm.

of the holotype, ANSP 51085 (see Figures 1, 2), reveals that it is identical with other large specimens of *Penitella* from Japan (Figures 3–6), and distinct from eastern Pacific specimens (Figures 7, 10–15) previously assigned to that species. Because there is no available name for the eastern Pacific species, it is described as new below. Descriptive terminology follows that of KENNEDY (1974:11–13, fig. 2).

The following institutional abbreviations are used: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; CAS, California Academy of Sciences, San Francisco; LACM and LACMIP, Natural History Museum of Los Angeles County, Los Angeles (LACMIP, Invertebrate Paleontology; LACM, Invertebrate Zoology (Malacology)); MCZ, Museum of Comparative Zoology, Cambridge; NMC, National Museum of Natural Sciences, Ottawa; NSMT, National Science Museum, Tokyo; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara; SDSNH, San Diego Museum of Natural History, San Diego; SU, Stanford University, Stanford (collections at CAS); UCLA, University of California, Los Angeles (collections at LACM and LACMIP); UCMP, University of California Museum of Paleontology, Berkeley; UMUT, University Museum, University of Tokyo, Tokyo; and USNM, U.S. National Museum of Natural History, Washington.

SYSTEMATICS

Family PHOLADIDAE Lamarck, 1809

Subfamily MARTESIINAE Grant & Gale, 1931

Genus *Penitella* Valenciennes, 1846

Type species: *Penitella conradi* Valenciennes, 1846, by subsequent designation (GRANT & GALE, 1931:433).

Western Pacific

Penitella gabbii (Tryon, 1863)

(Figures 1–6)

Zirphaea Gabbii TRYON, 1863:144, pl. 1, fig. 1.

Z.[*irphaea*] *Gabbii:* GABB, 1869:52, 88, in part; not pl. 15, fig. 10; (*Penitella gabbii* [holotype], in part *Zirfaea pilsbryi* [fossils], and *Chaceia ovoidea* [figured specimen]).

Penitella gabbi: TURNER, 1955:87, in part, pl. 53, fig. 2 [holotype]; not p. 85, pls. 52, 53 (fig. 1), 54; (*Penitella gabbii* [references to and figure of holotype], in part *P.* ***richardsoni*** [most records], and *P. turnerae*).

not *Penitella gabbi:* TURNER, 1962:306 (= *Penitella turnerae*); ADEGOKE, 1967:16 (=*Penitella* ***richardsoni*** [modern records], and *Zirfaea pilsbryi* [fossil records]).

not *Zirfaea gabbi* (Tryon) *femii* ADEGOKE, 1967:17 (*nomen nudum*, manuscript name); ADEGOKE, 1969:154, "fig. 6A"; pl. 9, figs. 2, 8, 11–12; pl. 10, figs. 3, 5–6, 13. [Both = *Zirfaea pilsbryi*.]

not *Penitella gabbii:* KENNEDY, 1974:45, figs. 36–40; HADERLIE & ABBOTT, 1980:392, fig. 15.77; pl. 127, fig. 15.77. [Both = *Penitella* ***richardsoni***.]

Diagnosis: Moderately large species of *Penitella,* adult length to 7.2 cm, but more frequently 5–6 cm in length. Callum complete, barely protrudes beyond beaks. Umbonal reflection flared, free anteriorly, lightly appressed over umbones. Periostracal attachment scars present within siphonal opening. Siphonoplax lacking.

Penitella kamakurensis (Yokoyama, 1922) and *P. chishimana* (Habe, 1955) are very similar to *P. gabbii,* if not synonymous; *P. kamakurensis* of authors, not YOKOYAMA (1922), differs in its smaller size, partial (incomplete) callum, reduced anterodorsal margin (which is not concave as in *P. gabbii*), appressed umbonal reflection, more lobate dorsal extension of callum, and leafy periostracal fringe on posterior margin.

Description: Adult shell oval in outline, moderately light in structure, reaching 7.2 cm in length (LACM 129158), but more often 5–6 cm long. Immature specimens beaked, widely gaping anteriorly; pedal gape closed by complete callum in adult; rounded and closed posteriorly. Anterior slope sculptured by close-set, upturned undulating concentric ridges, and radial "ribs" formed by aligned undulations of the ridges. Umbonal-ventral sulcus prominent, with ladderlike or steplike appearance due to inter-ridge depressions between upturned concentric ridges where they cross sulcus. Undulations reduced and finer near sulcus, where ridges bend in sweeping curve as they approach and cross sulcus. Disc and posterior slope sculptured by concentric growth lines and low rounded ridges that are extensions of those on the anterior slope.

Umbones prominent, located near anterior third of shell. Anterodorsal margin distinctly concave between umbones and beaks. Umbonal reflection relatively narrow, flaring, free anteriorly with gap between it and anterior slope, loosely appressed over umbones. Dorsal extension of callum narrow, not lobate.

Mesoplax unknown.

Umbonal-ventral ridge distinct, often with beaded appearance due to internal expression of intersection of sulcus and concentric ridges. Muscle scars visible, generally smooth. Ventral muscle scar long, narrow, overlaps umbonal-ventral ridge. Posterior muscle scar elongate-oval in outline. Pallial sinus broad, extends to or just beyond umbonal-ventral ridge. Apophyses flattened, with gentle curvature, not bladelike, rotated 40–50° from long axis of shell, protruding at angle distinctly anterior to that of umbonal-ventral ridge.

Periostracum usually worn off disc region, dark brown on posterior slope; posterior margin without leafy periostracal fringe. Siphonoplax lacking. Periostracal attachment scars present inside siphonal opening. Anatomy unknown.

Holotype: Of *Zirphaea gabbii* Tryon, ANSP 51085. Dimensions: length, 56 mm; height, ca. 30 mm.

Type locality: "Coast of Japan?" (TRYON, 1863:144; see also comments of GABB (1869:53) quoted in the Introduction). Subsequent restriction of the "type locality" to Mon-

terey Bay, California by TURNER (1955:87) is invalid because it was based on specimens of *Penitella* ***richardsoni*** sp. nov. rather than of *P. gabbii.*

Distribution: Based on a limited number of species lots in North American institutions, *Penitella gabbii* ranges on the Pacific coast of Japan at least from northeastern Honshu to southwestern Kyushu; its actual distribution is certainly more extensive.

HONSHU: Miyagi Prefecture: Hanabuchi, Hichigahama-machi (38°18'N) (LACM 129158). Fukushima Prefecture: Matsukawa-ura (37°39'N) (LACM 140430); Yotsukura coast (USNM 563670); Onahama-ura (36°57'N) (CAS 028806 [*ex* SU 46368]). KYUSHU: Nagasaki Prefecture: Nagasaki (32°45'±10'N) (USNM 249277).

Remarks: The Recent and fossil species of *Penitella* in the northwestern Pacific region, Japan and far eastern USSR, are in taxonomic disarray and in need of revision. *Penitella gabbii,* however, has priority over all existing nominal taxa. *Penitella kamakurensis* (Yokoyama, 1922) and *P. chishimana* (Habe, 1955) are very similar to *P. gabbii,* if not synonymous with it; both taxa are poorly understood. *Penitella chishimana* was based on two specimens from the northern Kurile Islands, an unfigured right valve (holotype) 51.7 mm in length, and a smaller paired specimen (paratype) 29.9 mm in length, of which the exterior of the right valve and the interior aspect of the mesoplax were figured (HABE, 1955:23–24, pl. 7, figs. 8, 9; TAKI & HABE, 1955:12, pl. 2, figs. 9, 10). The line drawing of the paratype shows a heavy(?), somewhat irregularly shapen valve that may have been affected by boring into an indurated substrate, conditions that would also have affected the aspect of the umbonal reflection. The mesoplax is broadly angulate posteriorly.

The lectotype of *Jouannetia kamakurensis* (=*Penitella kamakurensis*), designated by OYAMA (1973:caption for pl. 56, fig. 6a–c; see also KENNEDY, 1974:48), is a Recent juvenile shell only 7.6 mm in length (YOKOYAMA, 1922: 120, pl. 6, fig. 10; K. Chinzei, *in litt.,* 26 October 1972). The anterior dorsal margin of the lectotype (UMUT CM21154; see ICHIKAWA, 1983) is similar in aspect to that of *P. gabbii,* but is proportionately longer and decidely more concave than in similar-sized specimens (*e.g.,* NSMT Mo64597) of the undescribed species that is most commonly illustrated as *P. kamakurensis* (*e.g.,* HABE, 1955:pl. 7, figs. 5, 6; TAKI & HABE, 1955:pl. 2, figs. 14, 15; HABE & KOSUGE, 1967:pl. 63, fig. 15; KURODA *et al.,* 1971:pl. 102, fig. 8; HABE & OKUTANI, 1975:144 [4 figs.]). The paralectotype of *P. kamakurensis* (CM21155) has not been figured. Alaskan specimens previously cited as *P. kamakurensis* by KENNEDY (1974:48, fig. 60) are *Penitella hopkinsi* Kennedy & Armentrout, 1989. The Chinese taxa, *Pholadidea* (*Monoplax*) *dolichothyra* Thang, Tsi & Li, 1960, and *P.* (*M.*) *acutithyra* Thang, Tsi & Li, 1960, are not synonyms of *Penitella kamakurensis* as has been suggested by BERNARD (1983:61).

Eastern Pacific

Penitella ***richardsoni*** Kennedy, sp. nov.

(Figures 7–15)

not *Z.*[*irphaea*] *Gabbii:* GABB, 1869:52, 88, pl. 15, fig. 10; (*Penitella gabbii* [type], *Zirfaea pilsbryi* [fossils], and *Chaceia ovoidea* [pl. 15, fig. 10]).

not *Zirfaea gabbi(i): auctt.*; (most = *Zirfaea pilsbryi*).

Penitella gabbi(i): auctt., in part; not *Zirphaea gabbii* Tryon, 1863.

Penitella gabbi: TURNER, 1955:85, in part, pls. 52, 53 (fig. 1), 54; not pl. 53, fig. 2; (*Penitella* ***richardsoni*** [most eastern Pacific records], *P. turnerae,* and *P. gabbii* [figured type]); ADEGOKE, 1967:16, in part (*Penitella* ***richardsoni*** [modern], and *Zirfaea pilsbryi* [all fossil records]).

not *Penitella gabbi:* TURNER, 1962:306 (=*Penitella turnerae*).

not *Zirfaea gabbi* (Tryon) *femii* ADEGOKE, 1967:17 (*nomen nudum,* manuscript name); ADEGOKE, 1969:154, "fig." 6A; pl. 9, figs. 2, 8, 11, 12; pl. 10, figs. 3, 5, 6, 13. [Both = *Zirfaea pilsbryi.*]

Penitella gabbii: KENNEDY, 1974:45, figs. 36–40 (contains synonymy for fossil records); HADERLIE & ABBOTT, 1980: 392, fig. 15.77; pl. 127, fig. 15.77.

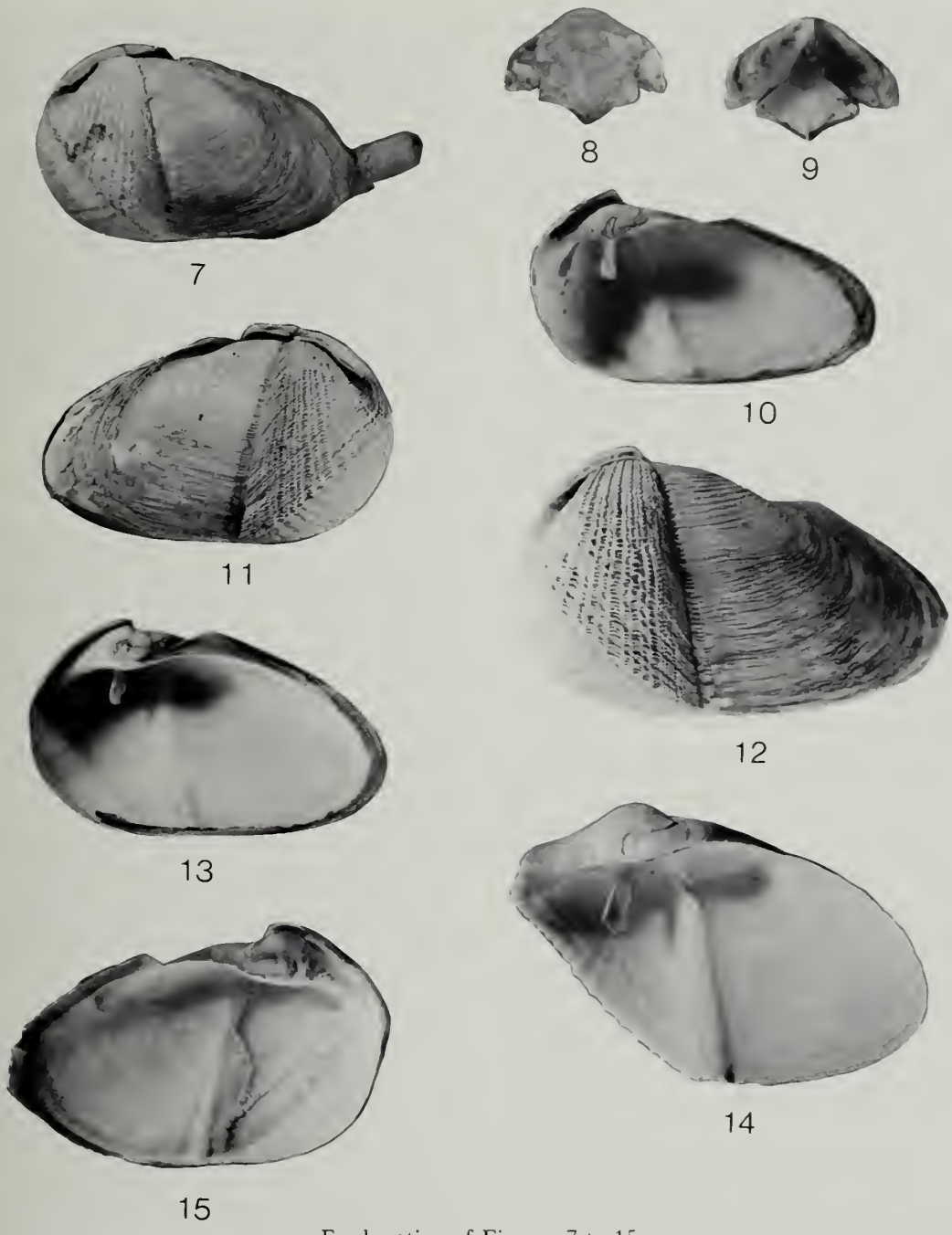
Diagnosis: Medium-sized species of *Penitella,* adult length to about 4.5 cm. Callum complete, does not protrude beyond beaks. Umbonal reflections narrow, lightly appressed over umbones, free anteriorly. Mesoplax with blunt, ventrally directed point and broad lateral wings posteriorly. Periostracum not present inside siphonal opening except as narrow marginal band. Siphonoplax lacking. Siphons creamy white, with "warty" protuberances.

Description: Adult shell oval in outline, moderately solid in structure, reaching 6 cm in length (LACM 86-239.1), but rarely exceeding 4.5 cm. Immature specimens beaked, widely gaping anteriorly, closed by complete callum in adult; rounded and closed posteriorly. Anterior slope sculptured by close-set, upturned, undulating, concentric ridges, and radial "ribs" formed by aligned undulations of the ridges. Umbonal-ventral sulcus prominent, marked by angular junction of concentric ridges of anterior slope and growth lines on disc. Disc and posterior slope sculptured with concentric growth lines and obscure, low, rounded ridges. Umbones prominent, located near anterior third of shell.

Umbonal reflection narrow, lightly appressed over umbo, free centrally and anteriorly. Callum complete, usually perfectly ovoid in shape, smooth or sculptured by weak radial extensions of sculpture of anterior slope, not protruding anterior to beaks. Dorsal extension of callum narrow, not lobate.

Mesoplax transverse, situated posterior to umbones, main body about as wide as long, truncate or pointed anteriorly, rounded posteriorly with a blunt, ventrally directed point, and with wide lateral wings posteriorly.

Umbonal-ventral ridge low, prominent in actively boring specimens, but inconspicuous in adults. Muscle scars visible, not roughened. Ventral muscle scar long, narrow,



Explanation of Figures 7 to 15

Figures 7–15. *Penitella* ***richardsoni*** Kennedy, sp. nov. Figure 7: LACM 2378, holotype, from Coon Creek, near Point Buchon, California (LACM sta. 84–22); shell length, 32 mm. Figures 8–10: SDSNH 53169, paratype, dorsal and ventral views of adult mesoplax (width, 8 mm) and right valve of same specimen (length, 34 mm); from Bolinas, Calif. Figure 11: SDSNH 53170, paratype, from Monterey Bay, Calif.; length, 41 mm. Figure 12: SBMNH 34955, paratype, from Del Monte Beach, Monterey Bay, Calif.; length, 49 mm. Figure 13: LACM 2381a, paratype, from Point Fermin, San Pedro, Calif. (LACM sta. 60-104); length, 34 mm. Figure 14: SBMNH 34956, paratype, same lot as Fig. 12; length, 49 mm. Figure 15: CAS 028804, paratype, from Del Monte Beach, Monterey Bay, Calif.; length, 44 mm.

overlaps umbonal-ventral ridge. Posterior muscle scar elongate-oval in outline. Pallial sinus broad, extends beyond umbonal-ventral ridge, sometimes to anterior margin. Apophyses flattened, not bladelike, rotated 20–25° from long axis of shell, wider ventrally, protruding at angle slightly anterior to that of umbonal ridge.

Periostracum moderately heavy, persistent, exists inside shell at siphonal opening only as narrow marginal band. Siphons creamy white in color, with small chiseled-appearing rectangular (not rounded), ridged "warty" protrusions that decrease in tuberosity and random orientation toward siphonal opening, where they are smaller, more closely spaced, and concentrically oriented. Inhalant and exhalant openings separate, ringed with papillae, exhalant opening one-third to one-quarter size of inhalant opening.

Holotype: Of *Penitella* ***richardsoni,*** LACM 2378, a live-collected specimen in alcohol, from LACM sta. 84-22, San Luis Obispo County, California. Dimensions: shell length, 32 mm; height, ca. 20 mm.

Paratypes: AMNH 104306 (2 specimens), Waterman, east of Port Orchard, Washington. CAS 028804 (figured specimen), and 065056 (1 specimen), both from 18 m (10 fms) off Del Monte Beach, Monterey Bay, Calif. LACM 2379 (1 specimen in alcohol), from LACM sta. 42-24 [AHF sta. 1466-42], Sunset Bay, Oregon; 2380a–e (5 dry specimens) from sta. 60-22, off Del Monte Beach, Monterey Bay, Calif.; 2381a, b (two specimens, 2381a figured) from sta. 60-104, Point Fermin, San Pedro, Calif.; 2382 (1 specimen) from sta. 61-111, Carpinteria, Calif.; 2383a, b (2 specimens) from sta. 66-2, Camalu-by-the-Sea, Baja California; 2384 a, b (2 specimens) from sta. 68-248, near Duxbury Reef, Bolinas Bay, Calif.; 2385 (1 specimen) from sta. 72-106, Middle Cove, Cape Arago State Park, Oregon; 2386a–e (3 dry specimens [2386a–c] and 2 specimens in alcohol [2386d, e]) from sta. 77-111, near South Point, Shell Beach, Calif. MCZ 189752 (1 specimen in alcohol), Culvers Point, San Juan Island, Washington; 195299 (4 specimens in alcohol), Whites Point, Palos Verdes Peninsula, Calif.; 278141 (3 specimens in alcohol), False Narrows, near Nanaimo, British Columbia. NMC 92791 [*ex* 45600] (1 specimen), Victoria, Vancouver Island, British Columbia. NSMT Mo64634, Mo64635 (2 specimens), Del Monte Beach, Monterey Bay, Calif. SBMNH 34955, 34956 (2 figured specimens), Del Monte Beach, Monterey Bay, Calif. SDSNH 53169 (figured by Kennedy, 1974: figs. 36–38), from Bolinas, Calif.; 53170 (figured by Kennedy, 1974:figs. 39, 40), from Monterey Bay, Calif. UCLA 20643 (4 specimens), from Tacoma, Washington. UCMP 38212 (1 specimen) from UCMP loc. B-6418, Scotts Creek, northwest of Santa Cruz, Calif. USNM 859330 [*ex* 334655] (2 specimens), Monterey, Calif.

Numerous lots of *Penitella* ***richardsoni*** were examined in the course of this study; unless listed above, they are specifically excluded from consideration as type material.

Type locality: LACM sta. 84-22, rocky intertidal zone, cove at mouth of Coon Creek, 0.6 km NNE of Point Buchon, south of Morro Bay, San Luis Obispo County, California (35°15′36″N, 120°53′48″W). Collected by C. Clifton Coney (CCC 84-9), 19 May 1984. Holotype associated with one specimen of *Penitella conradi* Valenciennes, 1846.

Distribution: Nanaimo and vicinity, east coast of Vancouver Island, Strait of Georgia, British Columbia, Canada (~49°10′±3′N) (MCZ 278140, 278141), to Sacramento Reef, just south of Isla San Geronimo, Baja California, Mexico (29°43′42″N) (Kennedy, 1974:46). I have not been able to confirm any of the published records of *Penitella "gabbii"* from Alaska (*e.g.,* Turner, 1955:88; Bernard, 1983:61). Specimens cited by Turner (1962) from the Queen Charlotte Islands, British Columbia, are *Penitella turnerae* Evans & Fisher, 1966.

Etymology: The species is named in memory of Richard A. Richardson (1948–1987), and is dedicated to his wife Judy and their son Justin.

Remarks: *Penitella* ***richardsoni*** is easily separated from all other eastern Pacific species of *Penitella* by its narrow umbonal reflection that is only lightly appressed over the umbo, but free centrally and anteriorly. Other differences are given in the diagnosis section, above. The holotype of *P. gabbii* (ANSP 51085; Figures 1, 2) from Japan is similar, but has a more flaring umbonal reflection, less angulate junction of the concentric sculpture across the umbonal-ventral sulcus, and periostracal attachment scars within the siphonal opening.

Although *Penitella* ***richardsoni*** is widely distributed and ranges at least from British Columbia to Baja California, it is not anywhere common, except perhaps in Monterey Bay, central California. Unconfirmed records of this species (as "*P. gabbii*") from Alaska may refer to *P. hopkinsi,* which has a mesoplax similar to that of *P.* ***richardsoni.*** At least one fossil record of "*P. gabbii*" (Pleistocene, Fivemile Point, Oregon, LACMIP loc. 3950) is reallocated to *P. hopkinsi.* Additional confirmed locality records of *P.* ***richardsoni*** from the Pleistocene include the second and tenth terraces on San Nicolas Island, off southern California (LACMIP loc. 11751 and UCMP loc. D-9616, respectively).

Recently, Gazdzicki *et al.* (1982) reported a species of *Penitella* from Pliocene glaciomarine sediments of the Polonez Cove Formation (Siklawa Member) on King George Island, South Shetland Islands, Antarctica, which they (p. 732) compared to "*P. gabbi*" from the eastern Pacific. The specimens do not belong to *Penitella,* but represent one of the austral species of *Pholadidea* Turton, 1819.

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A New Species of Chimney-Building *Penitella* from the Gulf of Alaska (Bivalvia: Pholadidae)

by

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Abstract. *Penitella* ***hopkinsi*** sp. nov., from the Gulf of Alaska, differs from other species in the genus by its blunt and thickened posterior margin that inserts against the base of a chimney of agglutinated sediment (unique in the genus), by the shape of the mesoplax, and by details of the umbonal reflection and dorsal extension of the callum. Anatomy is unknown. Late Pleistocene records of the species range from the Seward Peninsula, Alaska, to Point Arena, California.

INTRODUCTION

Recent efforts to identify several enigmatic species of *Penitella* Valenciennes, 1846, from both the northeastern and northwestern Pacific revealed that a number of nomenclatural and taxonomic problems in the genus still need to be resolved (KENNEDY, 1985). Here we describe a new species of *Penitella* from the Gulf of Alaska region based on well-preserved modern (Recent) specimens collected by Armentrout in 1975 from the south end of Wingham Island. The specimens came from the modern intertidal marine abrasion platform that had been uplifted about 2.8 m during tectonic events associated with the 27 March 1964 Good Friday earthquake in Alaska (PLAFKER, 1969 [1970]: pl. 1; PLAFKER, 1974). Poorly preserved specimens (shells only) of this species previously had been cited as *Penitella kamakurensis* (Yokoyama, 1922), a Japanese species name that can now be dropped from eastern Pacific faunal lists. Descriptive terminology follows that of KENNEDY (1974a: 11–13, fig. 2).

The following institutional abbreviations are used: AMNH, American Museum of Natural History, New York; CAS, California Academy of Sciences, San Francisco; LACM and LACMIP, Natural History Museum of Los Angeles County, Los Angeles (LACMIP, Invertebrate Paleontology; LACM, Invertebrate Zoology [Malacology]); MCZ, Museum of Comparative Zoology, Cambridge; NMC, National Museum of Natural Sciences, Ottawa; NSMT, National Science Museum, Tokyo; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara; UCLA, University of California, Los Angeles (collections at LACM); UCMP, University of California Museum of Paleontology, Berkeley; USGS, U.S. Geological Survey, Menlo Park (M) and Washington; USNM, U.S. National Museum of Natural History, Washington.

DESCRIPTION

Family PHOLADIDAE Lamarck, 1809

Subfamily MARTESIINAE Grant & Gale, 1931

Genus *Penitella* Valenciennes, 1846

Type species: *Penitella conradi* Valenciennes, 1846, by subsequent designation (GRANT & GALE, 1931:433).

Penitella ***hopkinsi*** Kennedy & Armentrout, sp. nov.

(Figures 1–13)

Pholadidea penita (Conrad): MacNeil *in* MACNEIL *et al.*, 1943:73, 75, 94, pl. 16, figs. 4–6. [Not *Pholas penita* Conrad, 1837.]

Penitella kamakurensis (Yokoyama): KENNEDY, 1974a:48 (in part), fig. 60; (Alaska records only); KENNEDY, 1974b: 22 (in part; Alaska records only); BERNARD, 1983:61 (in part; eastern Pacific records only). [Not *Jouannetia kamakurensis* Yokoyama, 1922.]
Penitella kamakurensis of authors: KENNEDY, 1985:13.

Diagnosis: Medium-sized species of *Penitella,* adult length to about 4.5 cm. Posterior margin in adult shell blunt and thickened where it inserts against base of chimney (unique in *Penitella*). Siphonoplax lacking. Umbonal reflection not wide, loosely overlaps anterior slope, not tightly appressed as in *P. penita.* Callum complete, dorsal extension narrow, not lobate even in thick-shelled specimens. Mesoplax somewhat variable in shape, generally subrectangular, with medial constriction, bluntly pointed posteriorly, and with rounded, "swept-back" wings. Periostracum along commissure just posterior to mesoplax with small, opposing calcified patches; thin and light colored on disc and posterior slope. Anatomy unknown.

Penitella penita (Conrad, 1837) differs in its acutely pointed mesoplax, usually tightly appressed umbonal reflection, and flaplike siphonoplax; *P. conradi* Valenciennes, 1846, differs in its smaller size, rounded mesoplax, lobate and tightly appressed umbonal reflection, roughened muscle scars, cupped siphonoplax, and habit of boring into *Haliotis* shells; *P. fitchi* Turner, 1955, differs in its rounded mesoplax, tightly appressed umbonal reflection, shortened (reduced) anterodorsal margin, partial (incomplete) callum, and leafy periostracal siphonoplax; *P. turnerae* Evans & Fisher, 1966, differs in its large size, appressed umbonal reflection that is upturned at anterior end, and lack of a marginal periostracal band posteriorly; and *P. richardsoni* Kennedy, 1989, differs in its free, not appressed, umbonal reflection, and narrow dorsal extension of the callum.

Description: Adult shell medium sized for genus, reaching 5.5 cm in length (fossil, LACMIP loc. 11741), but rarely exceeding 4.5 cm; most adult shells are 3.5 to 4.5 cm in length. Elongate pear-shaped in overall appearance, more bulbous anteriorly, conically constricted posteriorly, with relatively straight dorsal and ventral margins. Immature specimens beaked, widely gaping anteriorly, closed by complete callum in adult; rounded and closed posteriorly. Posterior margin of adult shell blunt, where it inserts against base of chimney, thickened by buildup of periostracum from within. Siphonoplax lacking. Chimney of agglutinated sediment similar to that of *Parapholas californica* (Conrad, 1837); apertural opening circular in outline, basal opening bilaterally compressed with rimmed depressions on either side, where thickened end of shell inserts against base of chimney.

Anterior slope sculptured by close-set, upturned, undulating, concentric ridges, and radial "ribs" formed by aligned undulations of the ridges. Umbonal-ventral sulcus prominent, marked by angular junction of concentric ridges of anterior slope and growth lines on disc. Disc and posterior slope sculptured with concentric growth lines and obscure, narrow, rounded ridges.

Umbones prominent, located near anterior third of shell. Umbonal reflection not wide, loosely overlaps anterior slope, not tightly appressed as in *Penitella penita,* barely raised at anterior-most point. Callum complete, usually smooth, but sometimes with radiating furrows that correspond to undulations of the concentric ridges along the anterior margin, barely protruding anterior to beaks. Dorsal extension of callum narrow, not widely lobate in thick-shelled specimens, but may have greater height than lateral extent to compensate.

Mesoplax transverse, situated dorsally above and just posterior to umbones, somewhat more variable in shape than in some species, generally subrectangular, with medial constriction and rounded, "swept-back" lateral wings. Posterior end bluntly pointed, may be directed ventrally or posteriorly, but lacks sharpened appearance of that of *Penitella penita.* Ventrally, there may be a pocketlike fold posteriorly, which differs from the simple ridge found on the underside of the *P. penita* mesoplax.

Umbonal-ventral ridge low, not paticularly prominent in actively boring specimens, inconspicuous in adults. Muscle scars visible, smooth to barely roughened. Ventral muscle scar long, narrow, overlaps umbonal-ventral ridge. Posterior muscle scar elongate-oval in outline. Pallial sinus moderately broad, extends to or just beyond umbonal-ventral ridge. Apophyses somewhat irregular and bladelike, with flattened extremity, rotated somewhat from long axis of shell, wider ventrally, protruding at angle slightly anterior to that of umbonal-ventral ridge.

Periostracum on disc and posterior slope thin, light colored; thicker and dark brown around commissure, particularly at posterior extremity, and with small opposing calcified patches just posterior to mesoplax in adult specimens. Periostracal attachment scars may be present inside siphonal opening. Anatomy unknown.

Holotype: LACM 2387, from LACM sta. 75-582, Wingham Island, Alaska (type locality), coll. J. M. Armentrout, 1975. Dimensions: length, 41 mm; height, ca. 24 mm.

Paratypes: All from type locality unless otherwise indicated: AMNH 232083a, b (1 specimen and chimney). CAS 065057–065059 (3 specimens; Figures 10, 12, 13), 065060–065062 (3 chimneys; Figures 2–4). LACMIP 7864 (1 specimen) from LACMIP loc. 4816, Pleistocene, Point Arena, California (coll. G. L. Kennedy, 1974). LACM 2388a–c (3 specimens; Figures 5, 7, 9), 2388d–g (4 specimens with disassociated mesoplaxes), 2388h–k (4 specimens lacking mesoplaxes), 2388l–q (6 chimneys); LACM 2389a, b (2 specimens) from LACM sta. 65-180, Hinchinbrook Island, Alaska (coll. Rae Baxter, 1965). MCZ 297050a–c (1 specimen and 2 chimneys), 297064a, b (2 specimens), 297065 (chimney; Figure 1). NMC 92790 (1 specimen and chimney). NSMT Mo64636 (1 specimen and chimney). SBMNH 34961 (1 specimen). UCMP 38213 (1 specimen). USNM 859331, 859332 (2 right valves; Figure 6 [859331]) from USGS loc. M1627, Chi-

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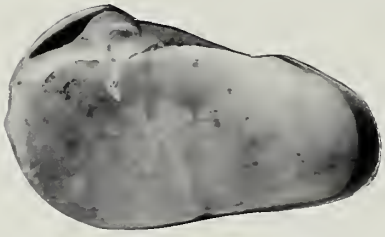

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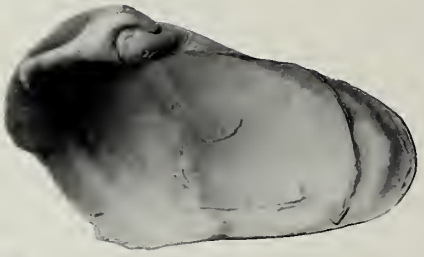

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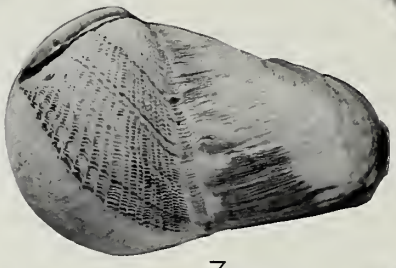

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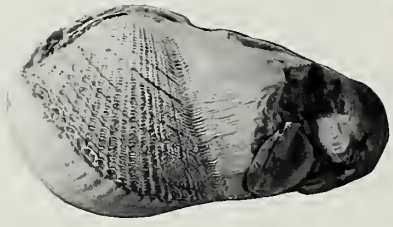

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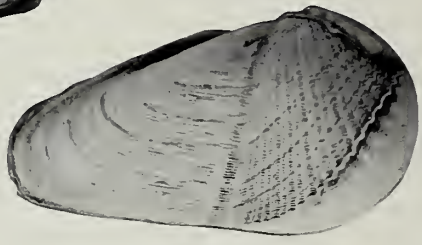

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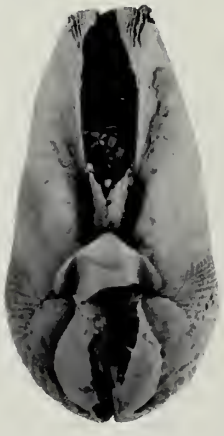

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rikof Island, Alaska (coll. unknown); USNM 859333 (1 specimen without mesoplax) from USGS loc. M3852, Middleton Island, Alaska (coll. George Plafker, 1968).

One unnumbered paratype and chimney remain in the collection of the junior author. Additional specimens cited below, mostly Pleistocene fossils, are specifically excluded from consideration as type material.

Type locality: LACM sta. 75-582. Southeast margin of modern emergent marine abrasion platform on southwest-facing southern end of Wingham Island, mouth of Controller Bay, Gulf of Alaska, Alaska (59°59′28.2″N, 144°22′36″W). Collected by John M. Armentrout, 16 July 1975. Association: holotype and 23 paratypes collected with nine *Penitella penita* (Conrad, 1837).

Modern distribution: ALASKA: Gulf of Alaska: Wingham Island (LACM sta. 75-582; type locality); Chirikof Island (USGS loc. M1627); Hinchinbrook Island (LACM sta. 65-180); Kayak Island (UCLA 35107); Middleton Island (USGS loc. M3852).

Fossil record: Neogene(?), Pleistocene.

NEOGENE(?): ALASKA: South end of Wingham Island, LACMIP Loc. 11741.

PLEISTOCENE: ALASKA: Second Beach, Peluk Creek, near Nome, Seward Peninsula, USGS locs. 3752 (MACNEIL, *et al.*, 1943:75, as *Pholadidea penita*), and 3751 (both KENNEDY, 1974a:48, as *Penitella kamakurensis*). South end of Wingham Island, USGS loc. 15864 (KENNEDY, 1974a: 48, as *Penitella kamakurensis* from "Yakutat Bay").

OREGON: Whiskey Run Terrace, north of Bandon at Fivemile Point, LACMIP loc. 3950 (KENNEDY, 1974a:47, 79, as *Penitella gabbii*; KENNEDY, 1978:387 (table 62), 504, as *Penitella* sp. cf. *P. gabbii*).

CALIFORNIA: Point Arena, near lighthouse, LACMIP locs. 4816 (KENNEDY, 1978:175 [table 11], as *Penitella* sp. indet.), and 10770.

Etymology: We are pleased to name this Alaskan species for David M. Hopkins, in recognition of his contributions to our understanding of the Quaternary history of Alaska, and of Beringia in particular.

Remarks: The first published record of this species was that of MacNeil (*in* MACNEIL *et al.*, 1943), who attributed several worn valves from the "Pliocene" [=Pleistocene] of the Seward Peninsula, Alaska, to *Pholadidea penita*. KENNEDY (1974a, b) recognized that these, and several Recent valves from the Gulf of Alaska, were specifically distinct, and introduced into eastern Pacific literature the Japanese species name *Penitella kamakurensis*. The fossil specimens were poorly preserved, only one possessed a mesoplax, and none was associated with the characteristic chimney. The thickened posterior margin was not particularly apparent on any of the existing specimens, modern or fossil.

The unusual nature of this chimney-building species was recognized only several years later, when the authors attempted to identify several well-preserved, but enigmatic specimens collected by Armentrout in 1975 in the Gulf of Alaska. Comparison of these specimens with those previously assigned to *Penitella kamakurensis* revealed them to be identical, and incorrectly assigned to *P. kamakurensis* as presently understood (see comments on Japanese species of *Penitella* in KENNEDY, 1989).

Penitella ***hopkinsi*** is separated from all other eastern Pacific species of *Penitella* by the chimney of agglutinated sediment, the blunt and thickened posterior extremity of the valves (which insert against the base of the chimney), by the shape of the mesoplax, by details of the umbonal reflection and dorsal extension of the callum, and by the small calcified patches in the periostracum just posterior to the mesoplax in adult specimens. Chimneys of agglutinated sediment and/or fecal material previously had been known only in *Parapholas* Conrad, 1848, and *Aspidopholas* Fischer, 1887, in the Martesiinae, and in *Xylophaga* Turton, 1822, in the Xylophagainae (TURNER, 1955; KNUDSEN, 1961; KENNEDY, 1974a).

Incomplete or poorly preserved specimens of *Penitella* ***hopkinsi*** may be confused with either *P. penita* (Conrad), or *P. richardsoni* Kennedy (=*P. gabbii* of authors, not Tryon, 1863, which is a Japanese species). The umbonal reflection of *P.* ***hopkinsi*** only loosely overlaps the anterior slope, and thus could be interpreted as an aberrant *P. richardsoni*, which normally has a freer and more open dorsal reflection, or with an aberrant *P. penita*, which normally has a more tightly appressed umbonal reflection. The mesoplax of *P.* ***hopkinsi*** is also somewhat intermediate in form between that of *P. penita* and *P. richardsoni* and could be confused with either species.

←

Explanation of Figures 1 to 13

Figures 1–13. *Penitella* ***hopkinsi*** Kennedy & Armentrout, sp. nov.; all from type locality (Wingham Island, Alaska) unless otherwise indicated. Figures 1–4: MCZ 297065 and CAS 065060–065062, one apertural, two lateral, and one basal view of four siphonal chimneys; ×1.25. Figure 5: paratype, LACM 2388a, right valve; length 38 mm. Figure 6: paratype, USNM 859331, right valve, from Chirikof Island, Alaska (USGS loc. M1627); length 44 mm. Figure 7: paratype, LACM 2388b, left valve; length 40 mm. Figure 8: hypotype, USNM 189802, left valve of paired specimen, Pleistocene, from Wingham Island, Alaska (USGS loc. 15864); length 51 mm. Figure 9: paratype, LACM 2388c, right valve of paired specimen; length 41 mm. Figures 10–13: dorsal views of four paired specimens. Figure 10: paratype, CAS 065057; length 33.6 mm. Figure 11: holotype, LACM 2387; length 41 mm. Figure 12: paratype, CAS 065058; length 41 mm. Figure 13: paratype, CAS 065059; length 43 mm.

Specimens that closely resemble Gulf of Alaska specimens of *Penitella* ***hopkinsi*** are present in the U.S. National Museum of Natural History collections from the eastern USSR: Aniwa Bay (Zaliv Aniva) (USNM 404319) on the south end of Sakhalin, just north of Hokkaido, Japan, and from Bering Island (USNM 210780), presumably Ostrov Beringa in the Komandorskiye Ostrova, between Kamchatka and the westernmost of the Aleutian Islands, Alaska. Because of slight morphological differences between the northeastern and northwestern Pacific populations, the lack of any intervening records, and the lack of (known) chimneys associated with the western Pacific specimens, the two populations are treated as distinct for the time being. Further study of western Pacific *Penitella* species may clarify the systematic relationships of the two.

Previous citations of *Penitella kamakurensis* in Alaska (KENNEDY, 1974a, b) were based on published figures of *P. kamakurensis* of authors, not YOKOYAMA (1922), and which actually represent an undescribed species (KENNEDY, 1985, 1989) that is characterized by its rounded mesoplax, tightly appressed umbonal reflection, partial (incomplete) callum, and reduced leafy periostracal fringe on its posterior margin. Morphologically it is most similar to the eastern Pacific *P. fitchi* Turner.

Fossil records of *Penitella* ***hopkinsi*** encompass a greater geographic extent than the known modern range of the species (Gulf of Alaska), which, however, may be greater than indicated here. The largest collection of fossils is from the southern end of Wingham Island (LACMIP loc. 11741), from the marine abrasion platform uplifted at the time of the 1964 Alaska earthquake. These are probably of Neogene age, but could possibly be as young as Pleistocene, and be contemporaneous with those from Quaternary deposits overlying the marine terrace on the southeastern spur of the island (USGS loc. 15864) (see MARTIN 1908:46, pl. 5; MILLER, 1961:sheet 1). A specimen from the latter locality was figured by KENNEDY, (1974a:fig. 60) as *P. kamakurensis* from "Yakutat Bay," and is refigured here (Figure 8). Most of the specimens from LACMIP loc. 11741 are not well preserved, but a few show traces of the diagnostic chimney.

The remaining Pleistocene specimens all represent extralimital records. The northernmost specimens are from the Second Beach deposits near Nome, Alaska (MACNEIL *et al.*, 1943). The Second Beach deposits contain a number of extralimital southern (*i.e.*, warmer-water) species, and are correlated to the peak of the last interglacial period about 125,000 yr BP (substage 5e of the marine oxygen isotope record; D. M. Hopkins, pers. commun., 1988), when marine waters were slightly warmer (at least seasonally) than they are today. The southern records are from the Whiskey Run Terrace near Bandon, on the southern Oregon coast, and at Point Arena, on the northern California coast. The faunas at both of these localities contain a number of extralimital northern (*i.e.*, cooler-water) species, and have been correlated to a minor sea-level high stand that occurred about 82,000 yr BP (substage 5a of the marine oxygen isotope record; KENNEDY, 1978 and KENNEDY *et al.*, 1982), when marine waters were slightly cooler than they are today.

ACKNOWLEDGMENTS

We thank Diane M. Bohmhauer (USNM), Louie N. Marincovich, Ellen J. Moore, and John Pojeta (USGS), and Ruth D. Turner (MCZ) for arranging loans of material. Arthur B. Ford, Steven W. Nelson, and Jill Schneider (all USGS) helped in obtaining copies of Don Miller's Alaskan field notes and open-file map of Wingham Island. Photographic prints were made at The Darkroom, Sacramento, through the courtesy of Gene Kennedy. Finally, we thank Eugene V. Coan, James H. McLean, LouElla R. Saul, Ruth D. Turner, and Edward C. Wilson for reviews of the manuscript.

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NOTES, INFORMATION & NEWS

Twisting in *Trochus:* Defense Against Hermit Crabs?

by
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Gastropod mollusks are generally not regarded as rapidly moving animals. Indeed their locomotion is characterized as slow. However, rapid movements have been reported under special circumstances. Strombids execute short leaps when contacted by a potential predator (BERG, 1974) and a rapid twisting movement has been described for a number of genera (ANSELL, 1969; PHILLIPS, 1978). These rapid movements are elicited by contact chemical detection of potential predators.

While watching hermit crabs and a few live gastropods in a water table at the Hawaii Institute of Marine Biology, Oahu, Hawaii, I observed small hermit crabs being thrown several centimeters by the movement of individuals of *Trochus intexus*. This note reports several unusual features of this pattern.

Individuals of *Trochus intexus* executed rapid twisting movements when small hermit crabs made physical contact and started to crawl on the shell of the gastropod both in the laboratory and as the snails crawled on coral colonies in nature. Video records showed that the twisting was primarily around the columellar axis of the snail. The movement typically consisted of a move through a 30–40° arc in one direction, 40–60° back in the other direction, and return to the starting posture. The whole cycle of movement took about a half second, 0.4–0.6 sec for the 10 instances analyzed from video records.

To get a better idea of when twisting was executed, 30 individuals of *Trochus intexus* were placed in culture bowls, 10 to a bowl, and specimens of either *Calcinus seurati, C. laevimanus,* or a grapsid crab, *Metagrapsis* sp. were placed with them. The responses of snails to 25 instances of tactile contact between crab and snail were observed and recorded for each crab species as the crabs moved about the container. The hermit crabs elicited twisting in the majority of cases (72% for *C. seurati,* 92% for *C. laevimanus*) while the grapsid crab did not (4% of the cases). The hermit crabs were always dislodged from the snail's shell by the motion.

Attempts were made to elicit twisting by tactile input administered by the observer. After several failures, it was found that a very light touch (0.10–0.12 g in air, slightly less in water) with the end of a fine glass pipette (1.6 mm outside diameter) on the shell of a snail occasionally elicited a twist. Individual *Trochus intexus* were tested with 5 sec of touching after being in one of three conditions for 30 min: (a) control, no other organisms in the culture dish, (b) grapsid crabs in perforated containers in the dish, and (c) specimens of *Calcinus laevimanus* in a perforated container in the dish. The response of 30 individuals, each tested once under each condition, one condition per day per snail, were: (a) control: one twist elicited, (b) grapsid present: one twist elicited, and (c) hermit crabs present: 16 twists elicited. Two of the twists when the hermit crabs were present occurred when the pipette touched an attached rock oyster (*Chama isotoma*) living on the shell of the *Trochus*.

The observed behavior is similar in form to the twisting reported in trochids and other groups of gastropods (ANSELL, 1969). However, the circumstances of elicitation are unusual. The behavior pattern can be elicited by purely tactile input to a non-living part of the snail, its shell. In many other reports, chemical contact with part of the snail's living tissue is required (HOFFMAN, 1980). Secondly, tactile elicitation of the pattern is much more likely when the snail detects hermit crabs via olfaction, even though by itself hermit crab odor will not elicit the behavior pattern. Yet hermit crabs occupy snail shells only after the snail has been killed by other factors and cannot damage healthy gastropods (see HAZLETT, 1981), especially the small crabs used in these studies. The sizes of crabs that readily elicited twisting were much too small to inhabit the shells that were twisted even if they could have damaged the snail. Thus, while the olfactory priming results point to a functional connection with defense against hermit crabs, the reason for such a connection is unknown, in contrast to cases where the crab eliciting avoidance behavior is a known predator of adult snails (GELLER, 1982).

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Update on Feeding and Digestion in the Moon Snail *Polinices lewisii* (Gould, 1847)

by
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The moon snail *Polinices lewisii* (Gould, 1847) is a large intertidal and subtidal mesogastropod (Naticidae) of sandy beaches in the northeastern Pacific. It feeds on bivalves and occasionally other gastropods (McGinitie & McGinitie, 1968). First it probes down into the sand for the prey with the propodium, then, digging down to the prey, it grasps it between the propodium and mesopodium, and returns to the surface of the sand, so that a feeding moon snail may be detected by the presence of a cracked mound in the substratum (Bernard, 1967). The moon snail drills through the prey's shell with the radula, assisted by the acid secretions of the accessory boring organ (Bernard & Bagshaw, 1969). The proboscis is hydraulically inserted into the mantle cavity and the soft parts of the prey are eaten.

In a study of functional morphology and digestion in this species Reid & Friesen (1980) noted the presence of zymogen granules in a pancreas-like anterior portion of the esophageal gland. They suggested that proteolytic enzymes contained in the zymogen granules might be injected into the prey to partially predigest it. To test this hypothesis we collected 12 specimens of moon snail from Rathtrevor Beach, east Vancouver Island, British Columbia. These were found at different stages of feeding on a variety of bivalves that included *Macoma nasuta, Protothaca staminea, Saxidomus giganteus, Mya arenaria, Tresus nuttallii,* and *Clinocardium nuttallii.* An additional 19 individuals of *Polinices* were examined and returned, unharmed, to the beach.

To discover if proteolytic enzymes had been injected, prey tissues from the site of active feeding were sampled. Similar tissues from intact bivalves of the same prey species were also sampled as controls. Aqueous extracts of the test and control tissues were compared by starch gel electrophoresis as described by Reid (1966). The test samples were always identical to the control samples. Therefore the only proteolytic enzymes present were those of the prey, and the hypothesis of Reid & Friesen (1980) is refuted.

Bivalve prey that has been drilled by the moon snail is limp, and does not respond to touch. We explored the possibility that an injected esophageal gland secretion might have a pharmacological effect on the prey by testing an aqueous extract of the gland on the heart of *Tresus nuttallii.* There was no such effect, and we conclude that the condition of prey is due to suffocation, as suggested by Ricketts & Calvin (1939) and Bernard (1967). An identical effect results from sealing clams in seawater in cooled plastic bags for 12 h.

There is progressive diminution of the zymogen granules in the anterior esophageal gland as feeding continues, and the gland is depleted of granules by the time the prey has been consumed. Also, the proteolytic activity of the stomach during active feeding increases to approximately 100 units per mL, approximately 10 times the level found in the pooled samples of Reid & Friesen (1980). Thus it seems that the latter correctly suggested that esophageal gland secretions could contribute to gastric digestion. It should also be emphasized here that Reid & Friesen discovered that the zymogen granule proteolytic enzymes of the moon snail were produced in an inert, masked form and were trypsin-activated. It was also apparent to them that the larger portion of the esophageal gland was an organ of absorption and digestion. The complete depletion of the esophageal gland zymogen granules at the end of a meal, and the need for their regeneration before recommencing to feed, probably correlates with Bernard's (1967) observation that on average one moon snail consumed one clam every four days.

Further to our tale we found that the most common bivalve prey at Rathtrevor Beach was *Macoma nasuta,* and all of the prey had been drilled ventral to the umbo, sometimes the thickest part of the shell. This may be a consequence of the fact that in some instances, when the moon snail maneuvers the prey into a stable configuration for feeding, the bulge of the umbo is the closest part of the prey to the mouth parts. In this case feeding appears always to commence with the softest tissues, the digestive diverticula and gonad, but continues until all but the adductors are consumed. Bernard (1967) noted that *Protothaca staminea* was the favored prey in aquarium observations, but *Macoma nasuta* was not offered in his study. Only starving *Polinices* "ate the whole thing" (except the shell). Others left the adductors and sometimes the siphons. Twenty-five percent of Bernard's clam prey were consumed without drilling. Ricketts & Calvin (1939) and Reid & Friesen (1980) pointed out that feeding may proceed without drilling in bivalve prey that have a gape that exposes part of the mantle or siphonal tissue to direct attack by the radula. It may be a matter of chance whether the initial seizure of the prey leaves the umbones or the mantle margins closest to the mouth.

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1989 Centennial Meeting of the American Society of Zoologists

The 1989 Centennial Meeting of the American Society of Zoologists will be held in Boston, Massachusetts, from 27 to 30 December 1989. Scheduled are plenary lectures, oral papers, and poster sessions, as well as entertaining peripheral events such as the ASZ Symphony Orchestra.

The American Microscopical Society, Animal Behavior Society, The Crustacean Society, International Association of Astacology, and Society of Systematic Zoology will be meeting with the ASZ and helping to celebrate its anniversary.

The deadline for abstracts is 4 August 1989.

For more information contact:

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Frank Rheinhold Bernard, 1940–1989

Malacologists will be saddened to learn of the death of Frank Rheinhold Bernard on 29 March 1989.

Frank was born in August 1940, in Brussels, Belgium, the second son of an Austrian father and a Scottish mother. Frank spent his early years in Brussels, where he became fluently bilingual in English and French. He was subsequently educated in England following his mother's move there after the war, and in school developed a working knowledge in a number of other languages.

Emigrating to British Columbia after leaving public school, Frank had a short, but successful, career in banking in Prince George. However, preferring a more physically vigorous lifestyle, he returned to England to complete a commercial hard-hat diver course. He later worked briefly in the North Sea and Gulf of Mexico in oil exploration, and then as a SCUBA instructor in Spain. In 1964, he returned to British Columbia and joined the staff of the Pacific Biological Station (PBS) in Nanaimo, then part of the Fisheries Research Board of Canada (now part of the federal Department of Fisheries and Oceans). In his job as a diver technician in the Shellfish Program, Frank worked extensively under Dr. Daniel B. Quayle in faunistic surveys of the west coast. Encouraged by Dan to become involved in research, he completed his Bachelor's Degree and Ph.D., both at the University of London, England. His doctoral thesis, "Nutrition of *Crassostrea gigas* (Thunberg, 1795): an aspect of estuarine energetics," was completed in 1972.

As his academic qualifications improved, Frank was promoted from technician to biologist and, in 1974, to research scientist. Apart from one year on secondment to Ottawa as a program manager for the Environmental Protection Service, he continued working at PBS on the biology and harvest of commercial shellfish species. He became Head of the Shellfish Section in 1980, but was laterally moved to Head of the Salmon and International Section a year later. During his 5-year leadership, he significantly altered and improved the direction of research activities of this major research section. In 1987, he spent 6 months in Ottawa as Acting Director of the Biological Sciences Directorate, Department of Fisheries and Oceans. During this period, signs of his illness were first noticed, and consequently he returned to Nanaimo, where he assumed first an advisory role to the Regional Director of Science and then the responsibility of Branch Science Coordinator. He focused much of his energy on completing work in progress, but nevertheless managed to initiate a few new projects, such as a catalogue of the living marine bivalves of China and adjacent regions.

Frank's fisheries studies resulted in publications on a variety of species—including squids, gastropods, bivalves, echinoderms, crustaceans, and fish—and subjects—from sampling designs, life history features, and population assessments. He has a pelagic surface trawl named after him, recognizing his extensive work in its development. Frank has many papers currently in press, and a bibliography and list of the taxa he named is planned for presentation at a later date.

Frank initiated his taxonomic studies during his participation in Dan Quayle's faunistic surveys in the 1960s, and most of his work in this area was done on his own time. An avid gardener who specialized in growing temperate vine, shrub, and tree species, his garden was a mini-arboretum. He worked constantly, and for many years, would typically spend his day at the lab, garden until dark, read classical literature or work on taxonomy until 4–5:00 AM, before catching a few hours sleep prior to returning to the lab at 9:00 AM. His drive to challenge himself found many outlets. He remodelled his house overlooking the entrance to Departure Bay, obtained his commercial small plane pilot's license, and was a parachutist, a motorcycle racer, an antique collector, an army reservist, and a past president of the Nanaimo Society for the Prevention of Cruelty to Animals.

Frank's command of English was excellent, and he represented his views in a concise, forceful, and eloquent manner. Although fundamentally shy and reserved, he was outspoken when necessary and not afraid to state his opinions. He had a deeply held sense of propriety and loyalty, and was generous to friends in need. He frequently assisted friends and colleagues from his own personal resources when they had insufficient means to meet their needs.

He will be sorely missed by his many friends and colleagues, both in Nanaimo and around the world.

Glen Jamieson, Pacific Biological Station

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BOOKS, PERIODICALS & PAMPHLETS

A Revision of the Fossil and Living Gastropods Related to *Plesiotriton* Fischer, 1884 (Family Cancellariidae, Subfamily Plesiotritoninae n. subfam.)

by A. G. Beu & P. A. Maxwell. 1987. New Zealand Geological Survey, DSIR, P.O. Box 30-368, Lower Hutt, New Zealand. 140 pp. Price: $50.

In view of recent intensification of activity and heated controversy in higher classification of prosobranch gastropods, it is unfortunate that this monograph has been slow to achieve broad distribution and review. Beu and Maxwell have, from a primarily paleontological and conchological perspective, assembled a convincing set of arguments for segregating this poorly known complex of 11 genera (previously allocated among Ranellidae, Buccinidae, Fasciolariidae, and Colubraridae) as a new subfamily of Cancellariidae. Although the strongest argument for assignment to Cancellariidae is based on new knowledge of the radula of two living species, the generic- and species-level taxonomy is founded upon combinations of shell characters. This is appropriate to the systematic treatment of a group whose evolution is a matter of rich historical (fossil) evidence of short-lived extinct taxa.

Although the work emphasizes the Cenozoic record of New Zealand taxa, it is based on examination of a global record that traces the group from its ancient, Late Cretaceous (Maastrichtian) origins and continuous Tethyan Paleogene distribution to its more narrowly restricted modern distribution in the western Pacific.

The emphasis in this monograph is the alpha taxonomy and construction of a descriptive taxonomic framework. The quality of illustration is outstanding, especially in the detail of SEM illustration of shell microsculpture. Features such as intracalx bristles and fine granulation of the parietal area hold great potential as taxonomic characters. Shell morphology at this level of detail is as yet unexplored as a basis for hypotheses of relationships among those higher gastropod taxa in which convergence has been a traditional problem.

Although I find myself wishing that the authors had ventured into formal phenetic or cladistic analyses and hypotheses of intra-generic and -specific relationships, this is a greedy wish for frosting on a cake that is already rich in intellectual calories.

In view of the radular and geologic evidence suggesting a primitive relationship of this group to the familiar cancellariids, it would now be helpful to know more about the states of the two suites of characters of the anterior alimentary system that have served as autapomorphic characters of Cancellaroidea and of Neogastropoda respectively (see Taylor & Morris. 1988. Relationships of neogastropods. Pp. 167–179. *In:* W. F. Ponder (ed.), Prosobranch phylogeny. Malacological Review Supplement 4, 346 pp.).

Carole S. Hickman

Late Miocene Deep-Water Mollusca from the Stillwater Mudstone at Greymouth, Westland, New Zealand: Paleoecology and Systematics

by Phillip A. Maxwell. 1988. New Zealand Geological Survey, DSIR, P.O. Box 30-368, Lower Hutt, New Zealand. 120 pp. Price: $50.

There are few regions of the world that rival New Zealand for the richness and excellent preservation of its Neogene molluscan faunas and no country that has done so thorough and detailed a job describing, dating, and correlating its Neogene sequences.

It is therefore remarkable that Phillip A. Maxwell has been able to set a new standard of excellence in his treatment of an extraordinary deep-water molluscan fauna from the relatively isolated Greymouth region of Westland. The systematic portion of the monograph treats 174 species, 37 of which are new, and introduces two new genera. Critical evaluations of generic concepts and relationships in several families (notably Nuculanidae, Propeamussiidae, and Turridae) are of general malacological interest.

The volume has the added bonus of an unusually detailed and biologically informed treatment of the paleoenvironment and paleoecology. Consideration of the bathymetric setting is augmented by a perceptive critique of Hickman's method of "taxonomic structure analysis"; and the trophic analysis includes a trophic web reconstruction and sufficient data that it might well have been published as an independent contribution to knowledge of deep-sea paleobiology.

The illustrations are of high quality. Most of the taxa are illustrated with scanning electron micrographs that show interesting details of shell microsculpture.

Carole S. Hickman

New Zealand Mesozoic Bivalves of the Superfamily Trigoniacea

by C. A. Fleming. 1987. New Zealand Geological Survey Paleontological Bulletin 53, 104 pp., 11 pls., 16 text-fig. Publications Officer, New Zealand Geological Survey, P.O.

Box 30-368, Lower Hutt, New Zealand. Price: $50.00 plus postage and packing.

Trigonias, with their distinctive shapes and remarkable sculpture patterns, have always attracted attention. These very noticeable and collectible bivalves virtually disappeared from the fossil record at the end of the Cretaceous Period and were considered extinct, but in 1802 living trigoniids were found in modern Australian waters. These "living fossils" were cited by anti-evolutionists as evidence of God's creative handiwork and by pro-evolutionists as evincing nature's way. The later discovery of the Tertiary fossil trigoniid *Eotrigonia* in Australia made heavenly intervention unnecessary, although as Fleming indicates, systematists have not always agreed on the phylogeny of *Eotrigonia* and *Neotrigonia*. The fossil record suggests that trigoniids were becoming much less diverse elsewhere in the world in the later Cretaceous, but Fleming shows that their diversity in austral waters in the latest Cretaceous stage, the Maastrichtian, was at an all time high. Furthermore, several cosmopolitan genera persisted later than elsewhere into the Cretaceous of New Zealand.

Fleming began study of the New Zealand trigoniids in 1953 and by 1964 had written a history of the family Trigoniidae in the southwest Pacific, but was unable to complete this work until shortly before his death. The grouping of species by period into Triassic, Jurassic, and Cretaceous suggests a stratigrapher's bias; Fleming was, however, evidently deeply interested in the biogeography of the group and its evolutionary history, and he records the apparent invasions of New Zealand seas by European groups and the development of endemic species and genera through the Mesozoic. Fleming has opted for a pragmatic classification of some radially ornamented Triassic and Jurassic genera in Minetrigoniidae, although he recognizes the probability that if the family Trigoniidae is polyphyletic as suspected by Cox, 1952, and discussed by Newell & Boyd, 1975, some of these Minetrigoniidae are Trigoniidae. The classification of Cox, 1969, emphasizes hinge structure and splits trigoniids into two families, the Trigoniidae and the Myophoriidae. Newell & Boyd emphasize form and sculpture and consider that similar hinges have arisen through parallel modifications of hinge structures. Fleming substantially agrees with Newell & Boyd, except that he places *Neotrigonia* in the Trigoniidae rather than the Minetrigoniidae.

Systematic descriptions make up two-thirds of the paper. A total of 24 supraspecific taxa (including one new subgenus) are grouped into three families and seven subfamilies (one of which is new). More than 50 species and subspecies are described or discussed; of these, 27 are new and five, for which the material is inadequate, are unnamed. Great care has been taken to indicate age of occurrence and a 5-pp. appendix supplies locality data. The paper is well illustrated. In addition to the 48 named New Zealand Mesozoic species or subspecies figured, text-figures of type species for several genera or subgenera illustrate characteristics of these taxa. The plates are unusual for a paper published in 1987 in that they are largely reproduced from drawings by Mr. R. C. Brazier. However, they match well with the 24 figures reproduced from Woods, 1917.

This paper considerably advances our knowledge of this interesting bivalve group, its biogeography, and evolution. Any systematist involved with trigoniids will wish to own it, despite the steep price; those more tangentially interested would be pleased to find it in the library.

L. R. Saul

Abalone
Gross and Fine Structure

by GERRIT BEVELANDER. 1988. The Boxwood Press: Pacific Grove, California. 80 pp. ISBN: 0-940168-05-7. Price: $18.00 (plus 6% tax for California residents) and shipping charge.

This book is a very nice monograph covering the structure of abalone from the external features to ultrastructure, including gross anatomy and histology of the organs and tissues. It is reminiscent of the Liverpool Marine Biology Committee Memoirs in its informal presentation and anatomical detail.

The highlights of the book are the photo montages of transverse and frontal sections of the whole animal and selected organs. They permit an overview of transverse and frontal sections of the entire animal. These are complemented by transmission electron micrographs (TEM) of selected organs of abalone by Hiroshi Nakahara and of *Monodonta lineata* by Elizabeth Andrews. The quality of the photographs is somewhat uneven; several are not quite focused and a bit muddy. Color and an increase in magnification would have been useful additions to the montages.

There is only a cursory description of development, and no discussion of torsion. There are, however, very nice scanning electron micrographs of larval and juvenile shells that help to explain how the adult abalone attains its flattened form. There are no references later than 1984; and evidence from other species is used to interpret the micrographs, without stating that this is the case. The orientation of some of the figures is not immediately clear; some (but not all) are reversed right and left, and anterior is not always in the same direction. Nevertheless, the book should be extremely useful to anyone trying to understand the anatomical arrangement of prosobranch gastropods, and especially valuable to those who are trying to explain it to others. From the day I received the book I have used it with great success to help students identify and understand serial sections of related species of gastropods.

Janice Voltzow

A Classification of the Living Mollusca

assembled by KAY CUNNINGHAM VAUGHT; edited by R. TUCKER ABBOTT & KENNETH J. BOSS, 1989. xii + 195 pp. American Malacologists, P.O. Box 2255, Melbourne, Florida 32902-2255. Price: $21 hardcover, $17 plastic comb binding.

This handy compilation of the suprageneric names in the living Mollusca is destined to find a home on the desks of most malacologists, and our field has to thank an amateur malacologist for having undertaken the task.

Some years ago, Vaught saw the need for such a compilation to help collectors and professionals in arranging their collections, no other single source being adequate to the task. The late Myra Keen encouraged her in this endeavor, and the initial product was a looseleaf edition covering just the marine shelled Mollusca, published in Cuernavaca, Mexico, in 1980.

This new edition is a major improvement, not only in its scope, which now includes all the living mollusks, but also in the citation of many synonyms, production quality, and its key to important literature. One assumes that the assistance of Drs. Abbott and Boss was instrumental in its scope and accuracy.

Needless to say, there has long been a critical need for such a compilation, and those in charge of collections and those simply trying to track down where a genus fits into the greater scheme will find it a useful reference.

Like any compilation, one will find things missing or misplaced, and the authors solicit comments for future editions.

Gene Coan

Monograph of Living Chitons (Mollusca: Polyplacophora). Volume 2, Suborder Ischnochitonina. Ischnochitonidae: Schizoplacinae, Callochitoninae & Lepidochitoninae

by PIET KAAS & RICHARD A. VAN BELLE. 1985. E. J. Brill/Dr. W. Backhuys, Leiden. 198 pp., 76 figs., 40 maps. Bound, 98 guilders (about $38.50 U.S.).

Monograph of Living Chitons (Mollusca: Polyplacophora). Volume 3, Suborder Ischnochitonina. Ischnochitonidae: Chaetopleurinae, & Ischnochitoninae (pars.) Additions to Vols. 1 & 2

by PIET KAAS & RICHARD A. VAN BELLE. 1987. E. J. Brill/Dr. W. Backhuys, Leiden. 302 pp., 117 figs., 52 maps. Bound, 120 guilders (about $60.00 U.S.).

The publication of these two volumes, part of a projected 10-volume taxonomic review, further documents the extensive efforts of the authors in their study of the Recent Polyplacophora. The format established in Volume 1 (1985) is continued: for each species the authors present information about the type specimen, a synonymy, a detailed description, notes on distribution, and line drawings of isolated valves or whole animals, girdle elements, and various radular teeth.

Volume 2 includes 74 species of the ischnochitonid subfamilies Schizoplacinae, Callochitoninae, and Lepidochitoninae. Ten genera are covered, including *Callochiton* Gray, 1847, *Lepidochitona* Gray, 1821, and *Tonicella* Carpenter, 1873. Because of the number of Western Hemisphere species, the latter two genera are of special interest to North American malacologists. *Dendrochiton* Berry, 1911 (synonym: *Basiliochiton* Berry, 1918) is utilized as a subgenus of *Lepidochitona*. Extensive synonymies are noted for *Tonicella rubra* (Linnaeus, 1767) and *Tonicella marmorea* (Fabricius, 1780). *Tonicella saccharina* Dall, 1878, from Alaska is placed in *Juvenichiton* Sirenko, 1975, with *J. albocinnamomeus* Sirenko, 1975, from the Kurile Islands as a junior synonym. Taxonomic decisions by Kaas & Van Belle present some new problems. For example, in an extensive synonymy for *Callochiton castaneus* (Wood, 1815) they note that two Spengler (1797) names predate that of Wood; they erroneously conclude (p. 17) "that there is no reason whatsoever why the older name *dentatus* should not be restored," a conclusion that violates Article 23b of the *International Code of Zoological Nomenclature* (1985).

Volume 3, dedicated to the memory of the late Dr. Antonio J. Ferreira of California, continues with coverage of 106 species of the subfamiles Chaetopleurinae and Ischnochitoninae (in part), and the addition of 16 species not previously reviewed in the first two volumes. Major genera included are *Chaetopleura* Shuttleworth, 1853, *Stenoplax* Dall, 1879, and *Lepidozona* Pilsbry, 1892. The name for the common Panamic *Chaetopleura, C. scabricula* (Sowerby, 1832), a name that was resurrected by FERREIRA (1983. *Veliger* 25:205), is rejected in favor of *C. lurida* (Sowerby, 1832), the accustomed name for this species. *Stenoplax circumsenta* Berry, 1956, considered by FERREIRA (1983. *Veliger* 25:313) to be a junior synonym of *S. corrugata* (Carpenter *in* Pilsbry, 1892) is recognized as a valid species. *Tripoplax* Berry, 1919, is used as a subgenus of *Lepidozona*. *Ischnochiton bromleyi* Ferreira, 1985, from Barbados is placed in the genus *Connexochiton* Kaas, 1979, known previously only from the eastern Atlantic.

Shortcomings noted in my review of Volume 1 (BULLOCK, 1985. *Veliger* 29:135) remain through the third volume. Species within a group are presented geographically, not phylogenetically. *Stenoplax limaciformis* (Sowerby, 1832), for example, is treated in Volume 3 on page 141, but its Caribbean cognate, *S. purpurascens* (C. B. Adams, 1845), to which it is very closely related, is reported on page 153 where coverage of the western Atlantic species of *Stenoplax s.s.* begins. Information about type material of junior synonyms is usually not present, although such information would be of great help to others. Taxonomic keys to species

are rarely given, and there is an almost equal lack of comparative remarks. Discussion of evolutionary relationships among the species and comments on the family, generic, and subgeneric categories used are lacking.

A perusal of these volumes indicates clearly that polyplacophoran taxonomy of these groups is still primarily in a descriptive stage that has intensified over the last few decades, primarily owing to the efforts of Ferreira, Kaas, Van Belle, and Sirenko. This descriptive work, along with previous efforts of others, is well summarized in the present volumes. However, one is struck by the incompleteness of this taxonomy—not due to the neglect of Kaas & Van Belle, but in many cases to the present paucity of material for study. For example, 14 species of *Callochiton* are known only from their respective type localities, and many of these species are known only by the holotype. Other species have been collected only on a few occasions. Future polyplacophoran systematists will be challenged greatly as they proceed to elucidate phylogenetic relationships of a number of these groups.

The *Monograph of Living Chitons* series will be an indispensible part of all malacological libraries. The up-to-date taxonomic coverage, detailed descriptions, and truly outstanding illustrations by the senior author will provide an invaluable reference source for amateur as well as professional malacologists. This work will assist greatly in the identification of species and collection curation. Kaas & Van Belle, without doubt, have produced a series that must be considered the cornerstone of future taxonomic work in the Polyplacophora.

Robert C. Bullock

Observing Marine Invertebrates. Drawings from the Laboratory

drawings by DONALD P. ABBOTT and students, edited by GALEN HOWARD HILGARD. 1987. Stanford University Press: Stanford, California. 380 pp. Price: $29.50.

In my mind's eye I can still see the late Don Abbott sitting at the back of the main teaching laboratory of Hopkins Marine Station, smiling and looking intently through the microscope. Routinely, while we students in his course on marine invertebrates were studying the abundant laboratory material available for the day, so was he.

An essential part of the observation and learning process for Don, and his students, was to record carefully what had been seen, often in the form of drawings liberally sprinkled with notes on color patterns, function, and behavior. Don believed that something about recording information in a drawing helped students, including himself, to see and remember relationships, and also that one could not make a good drawing without really understanding the subject.

This book is a collection of drawings from the laboratory, done mostly by Don Abbott, with some by a few of his students. Galen H. Hilgard compiled and edited the drawings, which include many Pacific coast animals not previously illustrated in such useful detail. The book contains 373 pages of drawings, with 93 pages devoted to mollusks. All show the general rules, explicitly stated on page xviii, that Don applied to his drawings: (1) a sketch should try to simplify reality without distorting it too much, (2) clean, simple lines, all connected, are better than a lot of short, sketchy lines, (3) the relationships of parts to one another are of paramount importance, and (4) a certain "freehand" neatness is economical of time and useful, but an unlabeled drawing is not useful at all.

Don Abbott was a keen observer, an admirer of invertebrate form and function, and a dedicated teacher. This splendidly practical book is Don's last gift to students at all levels. Further, in lieu of paying royalties, Stanford University Press has agreed to keep the list price as low as possible. My only complaint is that the paper used in the book is too thin: drawings from the next page tend to show through and several pages of my copy almost immediately tore away from the spiral binding. Nevertheless, the book is a must for all those interested in marine invertebrates.

D. Phillips

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Manuscripts must be typed on white paper, 8½″ by 11″, and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e., not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

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a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* Veliger 4:132–134.

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Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

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Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

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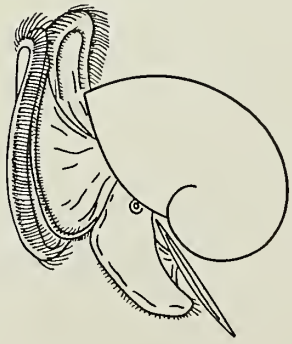

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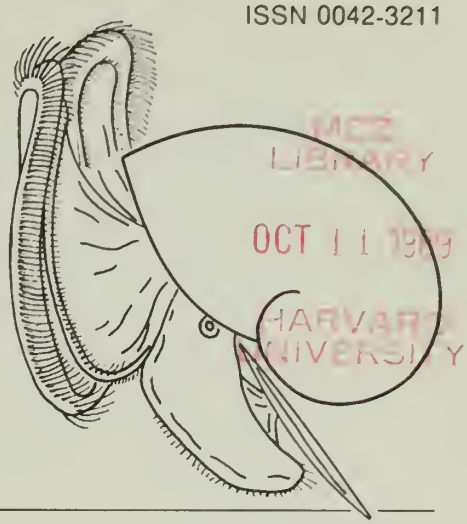

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Revision of the Gastropteridae (Opisthobranchia: Cephalaspidea) with Descriptions of a New Genus and Six New Species

by

TERRENCE M. GOSLINER

Department of Invertebrate Zoology and Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, USA

Abstract. Fifteen species of Gastropteridae are here recorded from the tropical Pacific and Atlantic oceans. Three of these are described as new species of ***Siphopteron*** gen. nov. and three as species of *Gastropteron*. *Sagaminopteron psychedelicum* Carlson & Hoff, 1974, and *G. bicornutum* Baba & Tokioka, 1965, are recorded from Papua New Guinea and their morphology is described. ***Siphopteron*** *pohnpei* (Hoff & Carlson, 1983) is recorded from the Hawaiian Islands. These constitute the first records of these species since their original descriptions. ***Siphopteron*** *brunneomarginatum* (Carlson & Hoff, 1974), known from Guam and Enewetak, is also recorded from Papua New Guinea. The morphology of an additional species from Easter Island is described. This probably represents an additional undescribed species, but inadequate material prevents its description here.

Additional aspects of the morphology of *Sagaminopteron bilealbum* Carlson & Hoff, 1973, *Sagaminopteron nigropunctatum* Carlson & Hoff, 1973, ***Siphopteron*** *flavum* (Tokioka & Baba, 1964) and ***Siphopteron*** *citrinum* (Carlson & Hoff, 1974) are described. The morphology of all species is described in order to present a more coherent picture of morphological variability within the family. This variability permits a phylogenetic analysis of the Gastropteridae and requires the description of ***Siphopteron***.

INTRODUCTION

The Gastropteridae had received little attention since the early works of Vayssière (1885) and Bergh (1893). Tokioka & Baba (1964), Baba & Tokioka (1965), and Baba (1970) rekindled interest and activity with the description of several species of Gastropteridae and a new genus from Japanese material. Minichev (1967) described an additional genus and species from China. Carlson & Hoff (1973, 1974) and Hoff & Carlson (1983) described several new taxa from the tropical western Pacific. Gosliner & Armes (1984), Gosliner (1984, 1988a), and Gosliner & Williams (1988) have added several other new taxa from various portions of the world's oceans.

On recent collecting trips to the Caribbean coast of Mexico, the Hawaiian Islands and Papua New Guinea, Michael Ghiselin and I have collected specimens of several species of Gastropteridae. These all constitute new records or undescribed species. Specimens of four previously described gastropterids were provided by Clay Carlson, Patty Jo Hoff, and Pauline Fiene. Additional specimens have been provided from collections made at Turks and Caicos islands in the Caribbean by Jeff Hamann, from Japan by the Royal Swedish Museum, and from Easter Island by Louis de Salvo. As little is known about the internal morphology of most members of the Gastropteridae, it is imperative to provide complete descriptions for all species, in order that comparative morphological studies can be employed to suggest phylogenetic relationships within the family.

DESCRIPTIONS

Sagaminopteron psychedelicum Carlson & Hoff, 1974

(Figures 1A, 2, 3)

Sagaminopteron psychedelicum Carlson & Hoff, 1974:354, text figs. 7–10, 12a, 13e, fig. 4).

Distribution: This species is known only from Guam and Pagan, Marianas Islands (Carlson & Hoff, 1974) and Papua New Guinea (present study). Dr. Maurice Jay (pers. comm.) has collected this species from Reunion Island, in the western Indian Ocean.

Material: One specimen, California Academy of Sciences, San Francisco, CASIZ 066549, dissected, harbor wall, Madang, Papua New Guinea, 22 m depth, 1 October 1986, T. M. Gosliner. One specimen, CASIZ 066550, dissected, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 20 October 1987, T. M. Gosliner. One specimen, CASIZ 066551, off Madang Resort Hotel, Madang, Papua New Guinea, 3 m depth, 1 February 1988, T. M. Gosliner. One specimen, CASIZ 066552, dissected, The Quarry, 30 km N of Madang, Papua New Guinea, 3 m depth, 12 February 1988, T. M. Gosliner. One specimen, CASIZ 066553, dissected, The Quarry, 30 km N of Madang, Papua New Guinea, 6 m depth, 14 February 1988, G. Williamson.

Natural history: Specimens of *Sagaminopteron psychedelicum* have been collected from shallow to relatively deep (22 m) rocky reefs. Animals were observed to swim in the laboratory. Though other members of the genus are known to feed on sponges (Carlson & Hoff, 1973; R. C. Willian, pers. comm.), specimens of *S. psychedelicum* have not been observed in association with any prey.

External morphology: The living animals (Figure 1A) were 3.5–12 mm in length. Their color is vivid and complex. The ground color of the head shield, parapodia, and visceral hump is pale green. A series of off-white and olive-green patches are present over the surface of the body. Each patch is encircled by a narrow well-defined line of black. The margins of the parapodia consist of a narrow inner black line followed by broad milky white band. The tip of the cream flagellum and anterior corners of the head shield are pale lavender. The apex of the siphon is orange. The gills are translucent white with opaque milky white flecks scattered over their surfaces.

The head shield is roughly triangular in shape, broadest anteriorly. The anterior ends are extended into two short, roughly triangular tentacles. The posterior end of the head shield is involuted into a siphon with a medial crest that terminates in a distinctly elevated apical papilla.

The parapodia are elongate and convoluted along their outer margin. They are relatively low, not covering much of the visceral hump, when the animal is actively crawling. The parapodia extend well beyond the visceral hump to the posterior end of the foot. The visceral hump is elongate and ovoid, comprising approximately two-thirds of the body length. On the posterior end of the visceral hump, just to the right of the median line, is a short conical flagellum. Several small ovoid tubercles are present on the posterior portion of the visceral hump. The ctenidium is tripinnate consisting of four distinct gills. Each gill is divided into approximately eight pinnae with approximately four pinnules per pinna. The foot is broad, not distinctly separate from the parapodia. A posterior pedal gland is visible on the ventral surface of the foot.

Digestive system: The buccal mass (Figure 2A) is short and highly muscular. The esophagus joins the buccal mass on the right side of the body. At this juncture is a pair of large, straplike, ventrally directed salivary glands. Within the buccal mass is a pair of jaws bearing several rows of rodlets (Figure 3A). Also contained within the buccal mass is the radula. Its formula in the largest specimen (CASIZ 066550) was 33 × 9–10·1·0·1·9–10. The inner lateral teeth (Figure 3B, C) are broad with an elongate, pointed cusp. The inner margin of the tooth bears two large triangular denticles. The second lateral teeth are broad with a single blunt denticle. The remaining outer laterals (Figure 3D) are curved with a single cusp and no other denticles. They become successively smaller towards the outer margin of the radula.

Central nervous system: The arrangement of ganglia (Figure 2B) is euthyneurous, with a short visceral loop. The cerebral ganglia are large and appressed to each other, without a distinct commissure. The pedal ganglia are as large as the cerebrals and are separated by an elongate commissure, which is ventral to the buccal mass. Posterior to the left cerebral ganglion are the left pleural, subintestinal, and visceral ganglia. From the visceral ganglion emanate the visceral loop and an additional visceral nerve. The visceral loop joins the posterior end of the suprantestinal ganglion on the right side of the head. An os-

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Figure 1

Living animals. A. *Sagaminopteron psychedelicum* Carlson & Hoff, 1974. B. ***Siphopteron*** *brunneomarginatum* (Carlson & Hoff, 1974). C. ***Siphopteron nigromarginatum*** Gosliner, sp. nov. D. ***Siphopteron*** *pohnpei* (Hoff & Carlson, 1983). E. ***Siphopteron quadrispinosum*** Gosliner, sp. nov. F. ***Siphopteron tigrinum*** Gosliner, sp. nov. G. *Gastropteron bicornutum* Baba & Tokioka, 1965. H. *Gastropteron* ***hamanni*** Gosliner, sp. nov. I. *Gastropteron* ***chacmol*** Gosliner, sp. nov.

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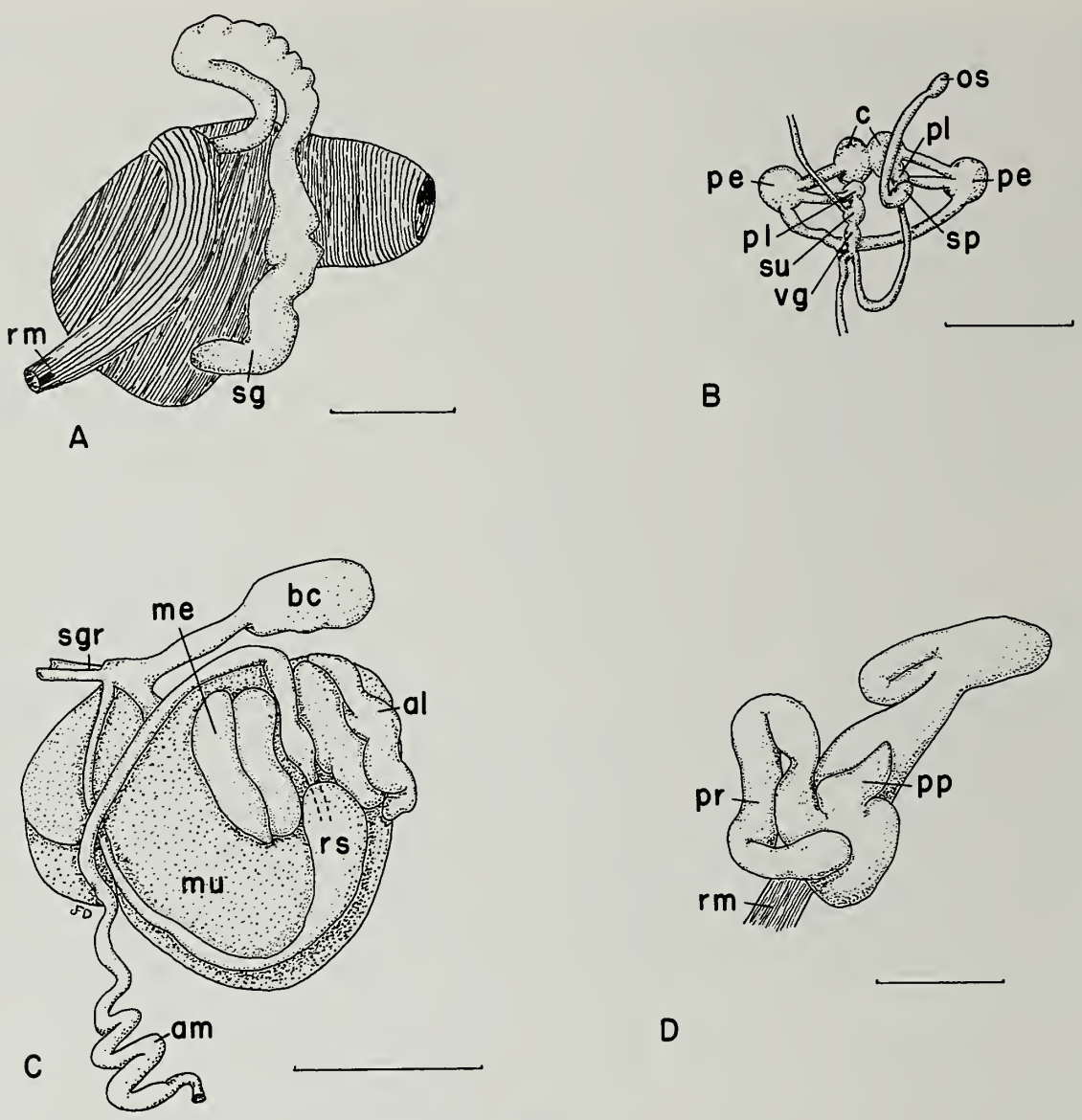


Figure 2

Sagaminopteron psychedelicum Carlson & Hoff, 1974. A. Buccal mass, scale = 0.5 mm. Key: rm, retractor muscle; sg, salivary gland. B. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglion; os, osphradial ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. D. Penis, scale = 0.5 mm. Key: pp, penial papilla; pr, prostate; rm, retractor muscle.

phradial nerve joins the supraintestinal and osphradial ganglia. The supraintestinal ganglion joins the posterior end of the right pleural ganglion.

Reproductive system: The detailed anatomy of the posterior reproductive system was examined in CASIZ 066553 (Figure 2C). Other specimens were immature or poorly preserved. One specimen (CASIZ 066550) was parasitized by a copepod, and the reproductive organs were poorly developed. The narrow, convoluted ampulla straightens into the hermaphroditic duct which curves around the surface of the large, lobate mucous gland. On the outer side of the gland mass, the hermaphroditic duct passes between the smaller, convoluted albumen and membrane glands. Near this point, the pyriform receptaculum seminis joins the hermaphroditic duct. The duct continues to the

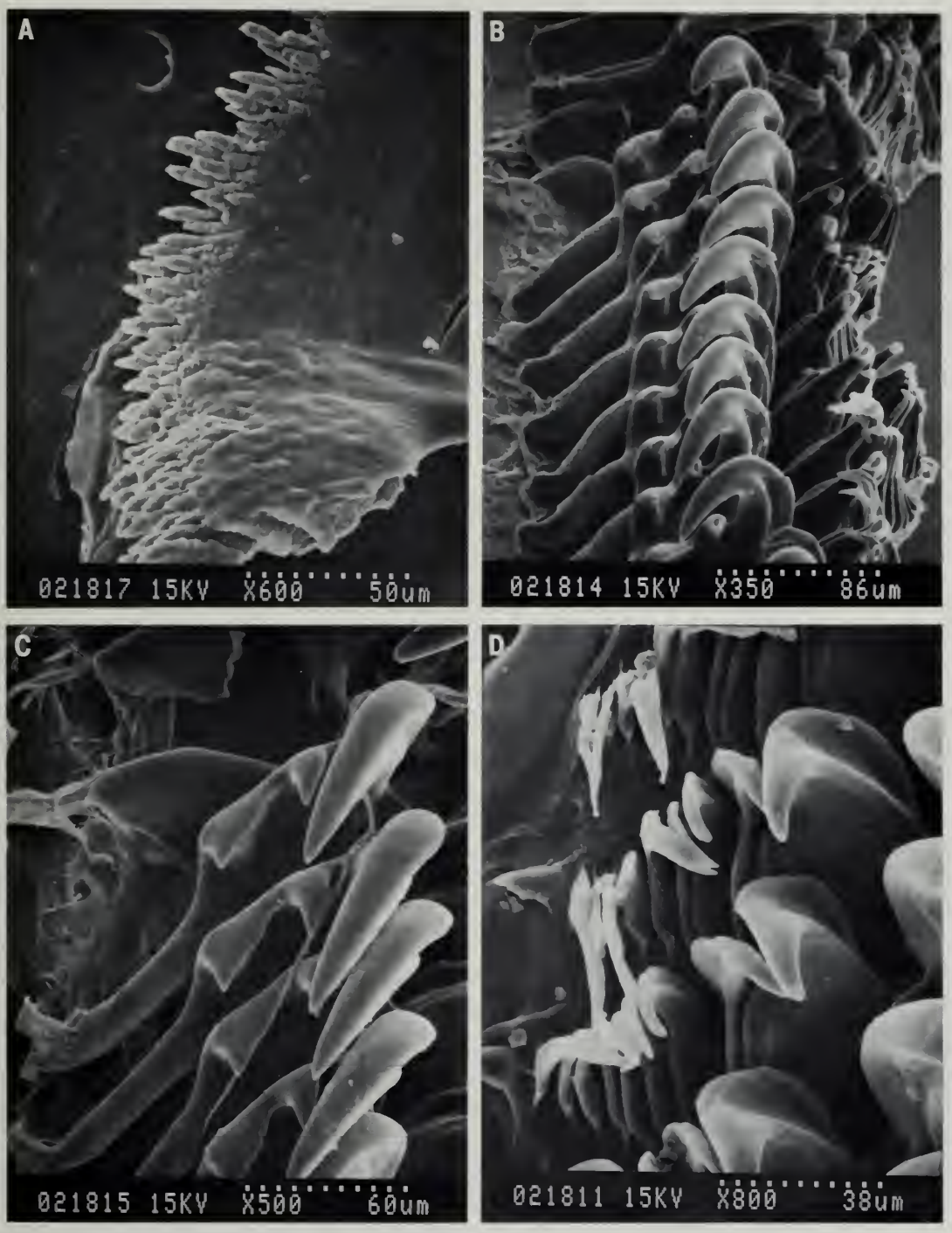


Figure 3

Sagaminopteron psychedelicum Carlson & Hoff, 1974. Scanning electron micrographs. A. Jaw elements. B. Half-row of radular teeth. C. Inner lateral teeth. D. Outer lateral teeth.

gonopore where it unites with the female glands and the short duct of the bursa copulatrix. From the gonopore, a ciliated sperm groove conducts spermatozoa to the penis, situated on the right side of the head.

The structure of the penis (Figure 2D) was determined in detail. The prostate is elongate and recurved. At its junction with the penial sac is a large retractor muscle. Within the penial sac is a simple, conical, unarmed papilla.

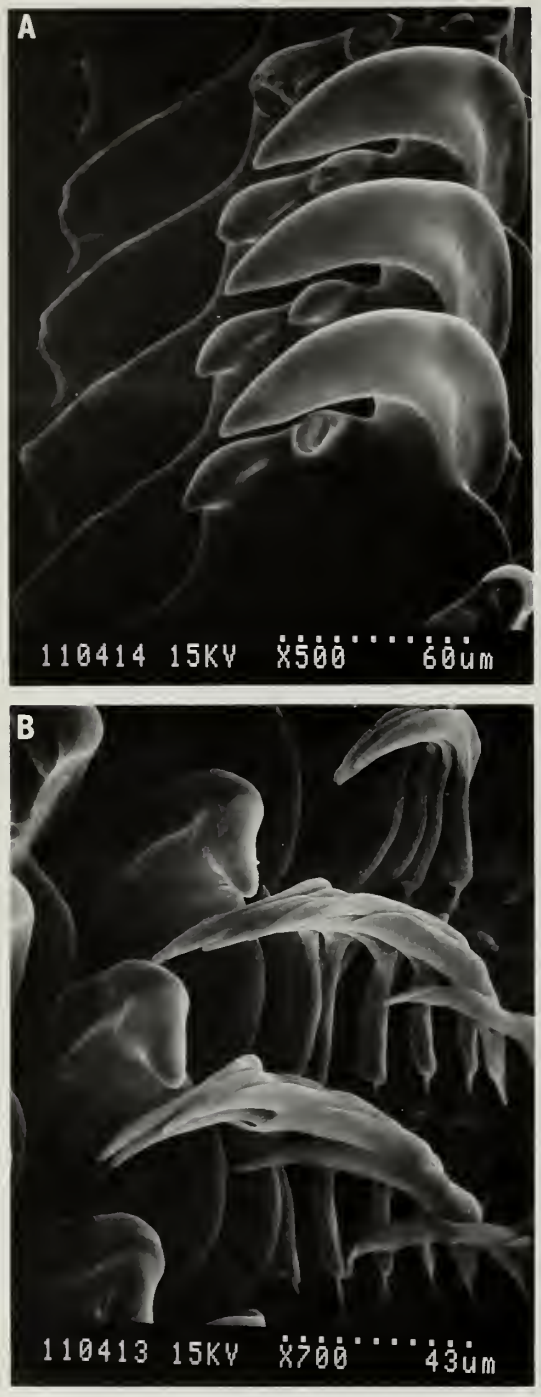


Figure 4

Sagaminopteron bilealbum Carlson & Hoff, 1973. Scanning electron micrographs. A. Inner lateral teeth. B. Outer lateral teeth.

Near the junction of the penis with the sperm groove is an expanded portion of the penis that may function as a spermatic bulb or for short-term sperm storage.

Discussion: The external morphology and coloration of the present material closely match those of the original description of *Sagaminopteron psychedelicum* Carlson & Hoff, 1974. The radula of the larger specimen examined here had slightly more rows of teeth, but otherwise corresponded to the original description.

Sagaminopteron bilealbum Carlson & Hoff, 1973

(Figures 4, 5)

Sagaminopteron bilealbum Carlson & Hoff, 1973:145, figs. 4–8, pl. 9, figs. 3, 4.

Material: Four specimens, California Academy of Sciences, San Francisco, CASIZ 066554, 066555, reef flat, Bile Bay, Merizo, Guam, 12 October 1988, C. H. Carlson and P. J. Hoff.

Distribution: This species is known only from Guam.

External morphology: The animals ranged from 3.5 to 12 mm in length. In aspects of their external morphology, they are identical to the original description.

Digestive system: The buccal mass is large and muscular. A pair of long, straplike salivary glands is present on either side of the esophagus. Near the anterior end of the buccal mass is the thin, cuticular jaw, which has longitudinal thickenings, but is devoid of rodlets. The radular formula in the 12-mm animal (CASIZ 066555) is 37 × 8·1·0·1·8. The inner lateral teeth (Figure 4A) have an elongate curved cusp with two large denticles on the inner face of the teeth. The second lateral teeth are broad with a single short cusp. The remaining outer lateral teeth are smaller than the inner ones and lack denticles other than the main cusp (Figure 4B). The teeth become increasingly narrow towards the outer edge of the radula.

Central nervous system: The arrangement of ganglia (Figure 5A) is similar to that observed in *Sagaminopteron psychedelicum*. The large cerebral ganglia are appressed to each other, without a distinct commissure. There are large, anteriorly directed ganglionic masses anterior to the cerebral ganglia. The pedal ganglia are approximately the same size as the cerebrals and are situated lateroventrally to them. The pedals are connected to each other by an elongate commissure and are joined to the cerebral and pleural ganglia by elongate connectives. Immediately posterior to the left pleural ganglion are the subintestinal and visceral ganglia. The visceral loop extends posteriorly from the visceral ganglion, recurves anteriorly, and joins the posterior end of the supraintestinal ganglion. The supraintestinal joins anteriorly with the right pleural ganglion.

Reproductive system: The reproductive system is monaulic (Figure 5B). The convoluted ampulla narrows into the hermaphroditic postampullary duct and curves around the perimeter of the large, ovoid mucous gland. It passes between the small albumen and membrane glands. In this region a pyriform receptaculum seminis joins the her-

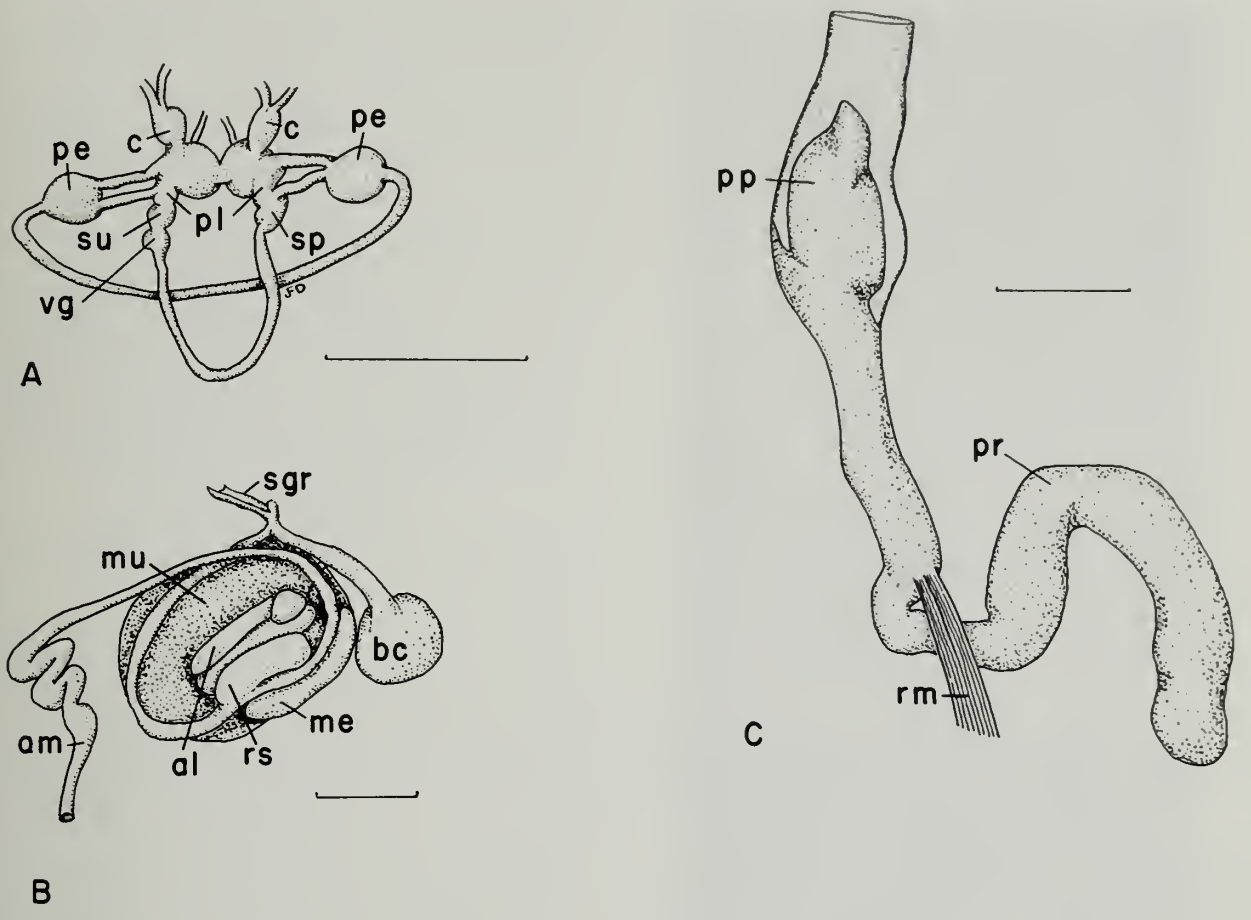


Figure 5

Sagaminopteron bilealbum Carlson & Hoff, 1973. A. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglion; pe, pedal ganglia; pl, pleural ganglia; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. B. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am; ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. C. Penis, scale = 0.25 mm. Key: pp, penial papilla; pr, prostate; rm, retractor muscle.

maphroditic duct. At this point the hermaphroditic duct widens somewhat and recurves to the hermaphroditic gonopore. The spherical, thin-walled bursa copulatrix joins the gonopore by means of a thin, straight duct. From the gonopore the ciliated sperm groove conducts endogenous sperm to the penis, situated on the right side of the head.

The penis (Figure 5C) has an elongate, slightly convoluted prostate. A retractor muscle is attached near the middle of the prostate. The penial papilla is simple, unarmed, and anteriorly rounded.

Discussion: This species is most similar to its congener *Sagaminopteron nigropunctatum* Carlson & Hoff, 1973. Though they are sympatric on different species of the same genus of sponges (Carlson & Hoff, 1973), *S. bilealbum* and *S. nigropunctatum* have several internal and external morphological differences. In *S. nigropunctatum* the parapodia are more reduced and this species is rarely observed swimming. This species also bears black spots and orange pigment on the rhinophoral crest and flagellum that are absent in *S. bilealbum*. Internally, the shell is proportionately larger in *S. nigropunctatum* than in *S. bilealbum*. In *S. nigropunctatum* the prostate is more highly convoluted and the penial papilla is more lobate than in *S. bilealbum*.

Sagaminopteron nigropunctatum Carlson & Hoff, 1973

(Figures 6, 7)

Sagaminopteron nigropunctatum Carlson & Hoff, 1973:141, figs. 1–3, 7, 8, pl. 9, figs, 1, 2.

Distribution: This species is known only from the type locality on Guam.

Material: Four specimens, California Academy of Sciences, San Franciso, CASIZ 066556, 066557, Bile Bay,

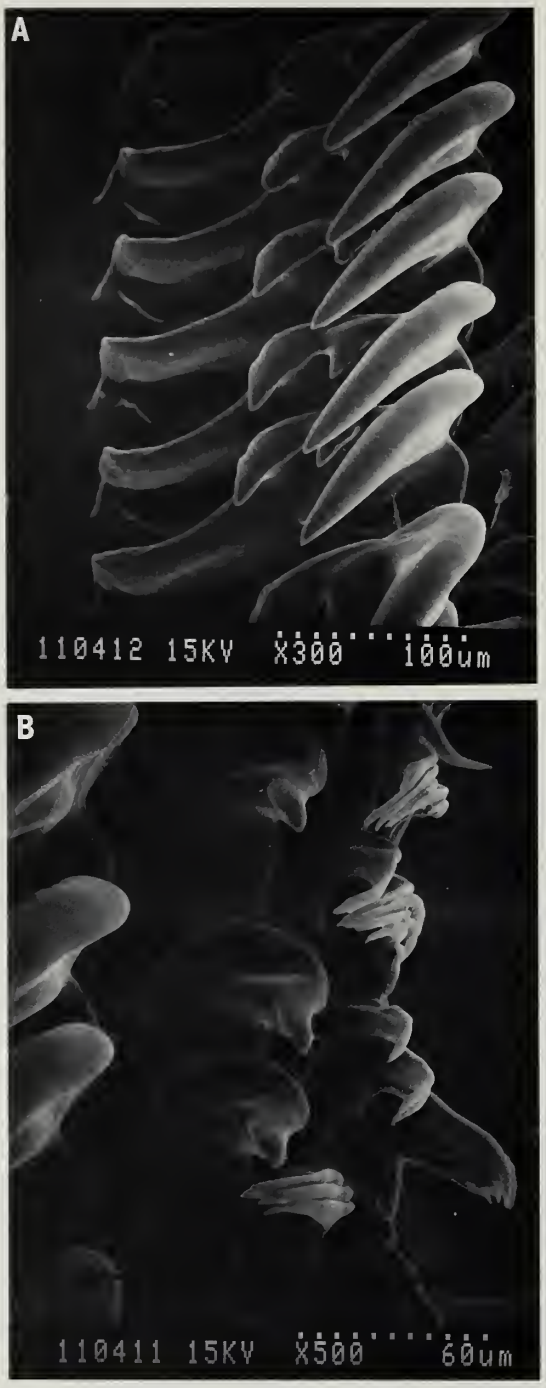


Figure 6

Sagaminopteron nigropunctatum Carlson & Hoff, 1973. Scanning electron micrographs. A. Inner lateral teeth. B. Outer lateral teeth.

Merizo, Guam, 1–3 m depth, 12 October 1988, C. H. Carlson and P. J. Hoff.

External morphology: The living animals were 3–10 mm long. In all aspects of their external morphology, they are identical to material described by Carlson & Hoff (1973).

Digestive system: The buccal mass is large and muscular. A chitinous lining is devoid of distinct jaw platelets. The radular formula in the 10-mm specimen (CASIZ 066557) was 32 × 9·1·0·1·9. The inner lateral teeth (Figure 6A) are broad with a large curved cusp and two smaller, triangular inner denticles. The second lateral tooth is smaller than the inner lateral, with only a single short cusp. The succeeding outer laterals (Figure 6B) are proportionately smaller and thinner than the second lateral, and become increasingly smaller towards the outer margin of the radula.

Central nervous system: The arrangement of ganglia is identical to that of *Sagaminopteron bilealbum*.

Reproductive system: The arrangement of organs (Figure 7A) is monaulic, and similar to the two preceding species. A large convoluted ampulla narrows into a post-ampullary hermaphroditic duct. The hermaphroditic duct curves around the margin of the large, lobate mucous gland and passes next to the smaller albumen and membrane glands. Here it joins the pyriform receptaculum seminis, and continues towards the hermaphroditic gonopore, where it joins the duct of the spherical bursa copulatrix, at the common gonopore.

The ciliated sperm groove terminates on the right side of the head, where the simple penis is situated. The penis (Figure 7B) has a large, convoluted prostate, which ends in a simple, lobed penial papilla. A retractor muscle is situated near the juncture of the penial papilla and prostate.

Siphopteron Gosliner, gen. nov.

Type species: *Siphopteron tigrinum* Gosliner, sp. nov., by original designation.

Etymology: ***Siphopteron*** is named for the prominent siphonal crest and parapodial "wings" that characterize members of the genus.

Diagnosis: Gastropteridae with or without an internal shell. Head shield small, roughly triangular, with well-developed siphonal crest, bearing a prominent dorsal ridge. Parapodia short or long and overlapping. Visceral hump roughly ovoid. Flagellum present or absent. When present, single on right side or terminal. Gill simple with many or few pinnae. Foot triangular posteriorly, with large pedal gland. Jaw platelets present or absent. Radula with 2–6 outer lateral teeth per side. Inner laterals large, with or without denticles. Cerebral commissure short or absent. Subintestinal and visceral ganglia distinct or fused. Penis

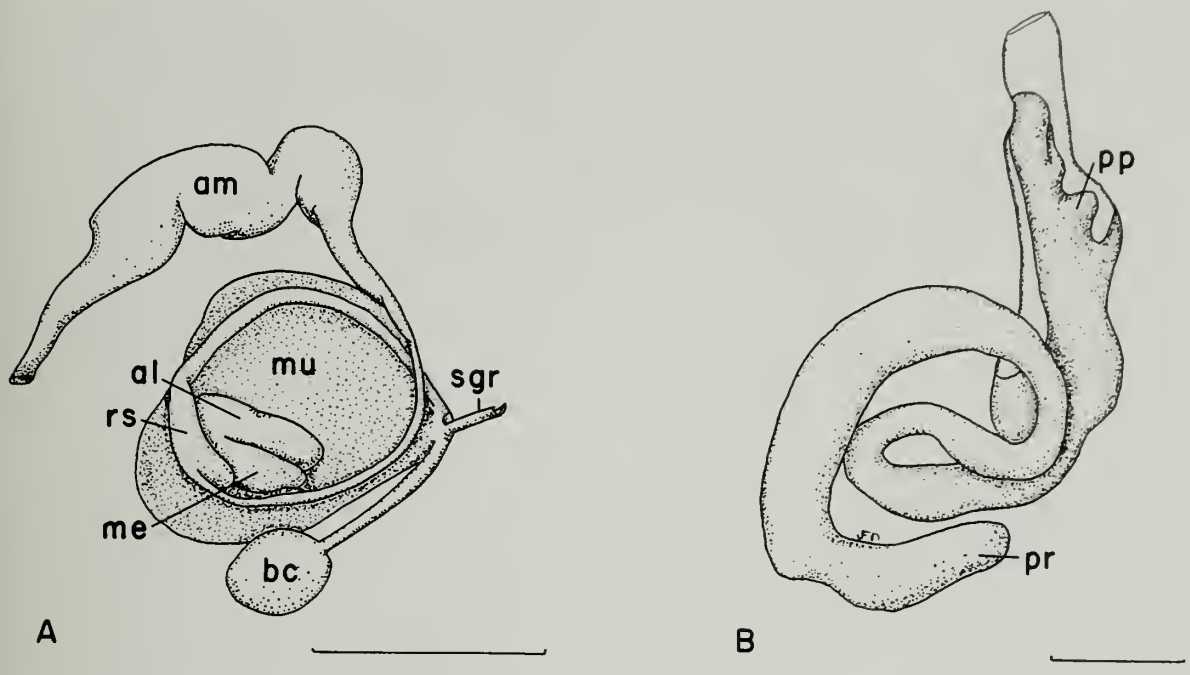


Figure 7

Sagaminopteron nigropunctatum Carlson & Hoff, 1973. A. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. B. Penis, scale = 0.25 mm. Key: pp, penial papilla; pr, prostate.

complex, with spermatic bulb or separate penial duct and bulb, often armed with rows of chitinous spines.

Siphopteron *brunneomarginatum* (Carlson & Hoff, 1974)

(Figures 1B, 8, 9)

Gastropteron brunneomarginatum Carlson & Hoff, 1974: 347, text figs. 1, 2, 12c, 13b, pl. X, fig. 1; Kay & Johnson, 1987:126.

Siphopteron *brunneomarginatum* (Carlson & Hoff, 1974) comb. nov.

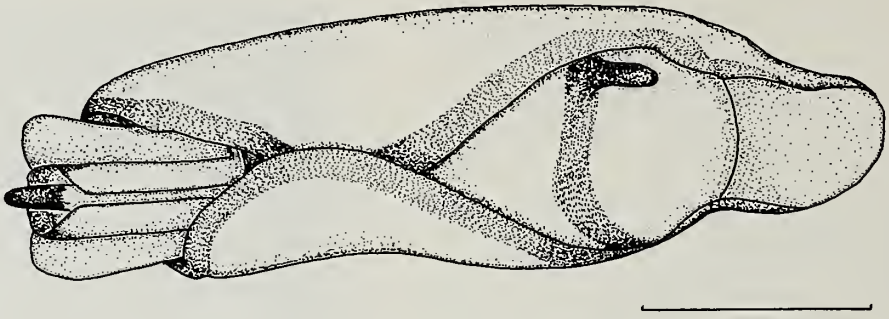
Distribution: ***Siphopteron*** *brunneomarginatum* has been recorded from the type locality, Guam (Carlson & Hoff, 1974), Enewetak Atoll (Kay & Johnson, 1987), and Papua New Guinea (present study).

Material: One specimen, California Academy of Sciences, San Francisco, CASIZ 064350, dissected, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 22 October 1986, T. M. Gosliner. Two specimens, CASIZ 064352, Barracuda Point, Madang, Papua New Guinea, 10 m depth, 12 October 1986, T. M. Gosliner. One specimen with egg mass, CASIZ 064359, Cement Mixer Reef, Madang Papua New Guinea, 2 m depth, 20 October 1986, T. M. Gosliner. One specimen, CASIZ 066358, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 20 October 1986, T. M. Gosliner. One specimen, CASIZ 066559, The Chimney, Madang, Papua New Guinea, 10 m depth, 30 January 1988, T. M. Gosliner. One specimen CASIZ 066560, dissected, Planet Rock, Madang, Papua New Guinea, 10 m depth, 28 January 1988, T. M. Gosliner. One specimen, CASIZ 066561, The Quarry, N of Madang, Papua New Guinea, 12 m depth, 11 February 1988, T. M. Gosliner.

Natural history: Specimens of this species have been observed on the underside of coral rubble on shallow-water reefs. This species has not been observed to swim, either in the field or laboratory.

External morphology: The living animals (Figure 1B) are 3–5 mm in length. The body is uniformly light greenish yellow with chocolate brown lines extending along the margins of the parapodia to the foot, as a transverse band on the visceral hump, which extends on to the flagellum, when present, and on the apex of the siphon.

The head shield (Figure 8A) is short and triangular with an involuted siphon at its posterodorsal end. The siphon contains a medial crest whose apex is slightly elevated above the rest of the siphon. The visceral hump is elongate and posteriorly rounded. An elongate, conical flagellum is present on the right side of the visceral hump, in four of the five specimens collected in 1986 and all of the 1988 specimens. It is entirely absent in the fifth 1986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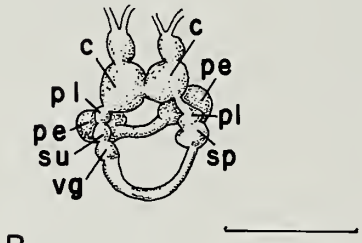
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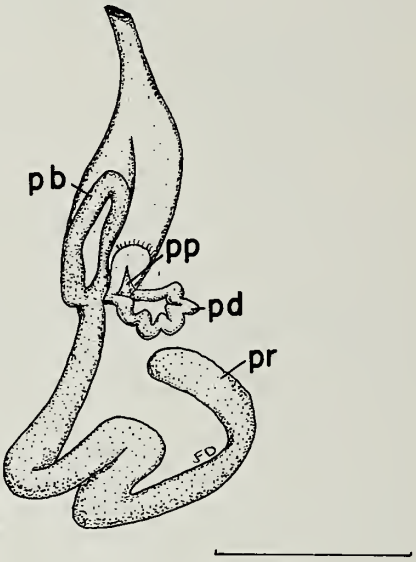
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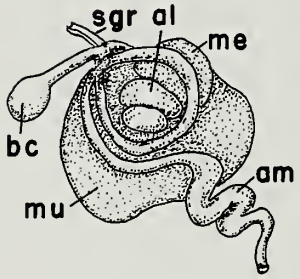
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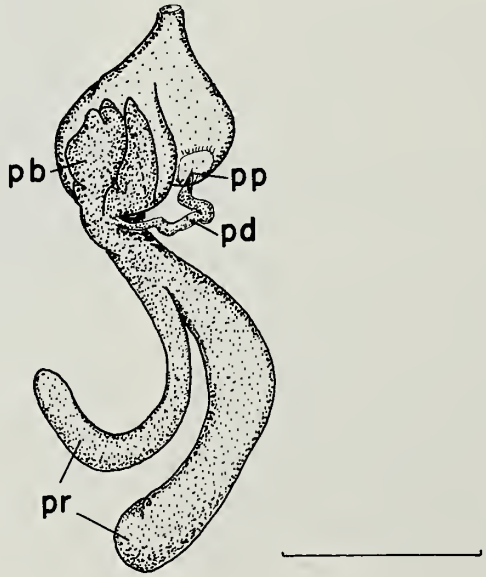
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specimen. The parapodia are elongate and high. Near the middle of the body the margins of the two parapodia touch or overlap each other. The gill is small and consists of 3 or 4 simple plicae.

Digestive system: A large ventral oral gland is present on the ventral side of the muscular buccal mass. An elongate, convoluted salivary gland is present on either side of the junction of the esophagus with the posterior end of the buccal mass. No distinct jaw platelets are present on the chitinous lining within the buccal mass. The radular formula was 23 × 3·1·0·1·3 in one specimen observed. The inner lateral teeth (Figure 9A, B) bear 5–7 small, irregular denticles along the inner margin of the elongate central cusp. The outer laterals (Figure 9A) are narrower and lack denticles other than the central cusp.

Central nervous system: The arrangement of ganglia is euthyneurous (Figure 8B). The cerebral ganglia are large and appressed to each other, without a distinct commissure. Dorsal to each cerebral ganglion is a slightly smaller concentration of nervous tissue. The eyes are situated at the end of short optic nerves, which emanate from the cerebral ganglia. Ventral to each cerebral ganglion is a slightly smaller pedal ganglion. The pedal ganglia are joined by a short commissure that passes under the ventral surface of the buccal mass. Each pedal ganglion is joined to a cerebral and pleural ganglion by short connectives. Immediately posterior to the left cerebral ganglion is the small left pleural ganglion. Posterior to it are the subintestinal and slightly larger visceral ganglia. From the posterior end of the visceral ganglion, the visceral nerve curves under the esophagus and crop and joins the supraintestinal ganglion on the right side of the body. Immediately anterior to the supraintestinal ganglion is the right pleural ganglion.

Reproductive system: The reproductive system is monaulic (Figure 8C). The ampulla is narrow and convoluted for most of its length. The hermaphroditic duct curves around the proximal portion of the female gland mass. No distinct receptaculum seminis was observed in either of the two specimens dissected. The albumen and membrane glands are encircled by a loop of the hermaphroditic duct. The hermaphroditic duct exits at the gonopore, adjacent to the sperm groove and the duct of the spherical, thin-walled bursa copulatrix.

The penis (Figure 8D, E) is complex in structure. Either one or two prostates are present. If two are present, one is thicker than the other. Both protates are elongate and curved or convoluted. At their distal end is a narrow, convoluted duct, which joins the penial papilla in the penial sac. Adjacent to the penial papilla is a larger fleshy papilla, which is entirely devoid of any chitinous spines. A narrow retractor muscle is present on the inner side of the penis at the junction of the prostate with the penial sac.

Discussion: The external and radular morphology of ***Siphopteron*** *brunneomarginatum* were described by CARLSON & HOFF (1974). Nothing in the present material differs from the original description, with the exception of the variability of the presence or absence of a flagellum in some of the present material.

The penial morphology is similar to several other Indo-Pacific taxa (GOSLINER & WILLIAMS, 1988; present study) in that a distinct narrow duct runs from the junction of the penial sac and prostate to the penial papilla. However, only ***Siphopteron*** *brunneomarginatum*, *S. citrinum*, and *S. pohnpei* (Hoff & Carlson, 1983) are known to lack rows of chitinous spines in the penial bulb. The three species differ in their coloration. ***Siphopteron*** *brunneomarginatum* is the only one of the three species that possesses dark brown parapodial margins. The other two lack contrasting pigment on the margins.

The denticles on the radular teeth of ***Siphopteron*** *pohnpei* are far more prominent than in *S. brunneomarginatum* or *S. citrinum*. Although the three species lack spines on the penial bulb, there are some other differences in the structure of the penis. In *S. brunneomarginatum* and *S. citrinum* the prostate is more elongate than in *S. pohnpei*. More significantly, in *S. brunneomarginatum* the narrow duct that leads to the penial papilla begins at the junction of the prostate and penial bulb, whereas in *S. pohnpei* the duct is connected with the distal end of the penial sac (Figure 14C). The penial duct of *S. citrinum* is much shorter and thicker than that of *S. brunneomarginatum*.

Siphopteron *citrinum* (Carlson & Hoff, 1974)

(Figures 10, 11)

Gastropteron citrinum CARLSON & HOFF, 1974:350, text figs. 3, 4, 12d, 13c, pl. 10, fig. 2.
Siphopteron *citrinum* (Carlson & Hoff, 1974) comb. nov.

←

Figure 8

Siphopteron *brunneomarginatum* (Carlson & Hoff, 1974). A. Living animal, scale = 1.0 mm. B. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 0.25 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; sgr, sperm groove. D. Penis with undivided prostate, scale = 0.5 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate. E. Penis with bilobed prostate, scale = 0.5 mm. Lettering same as in D.

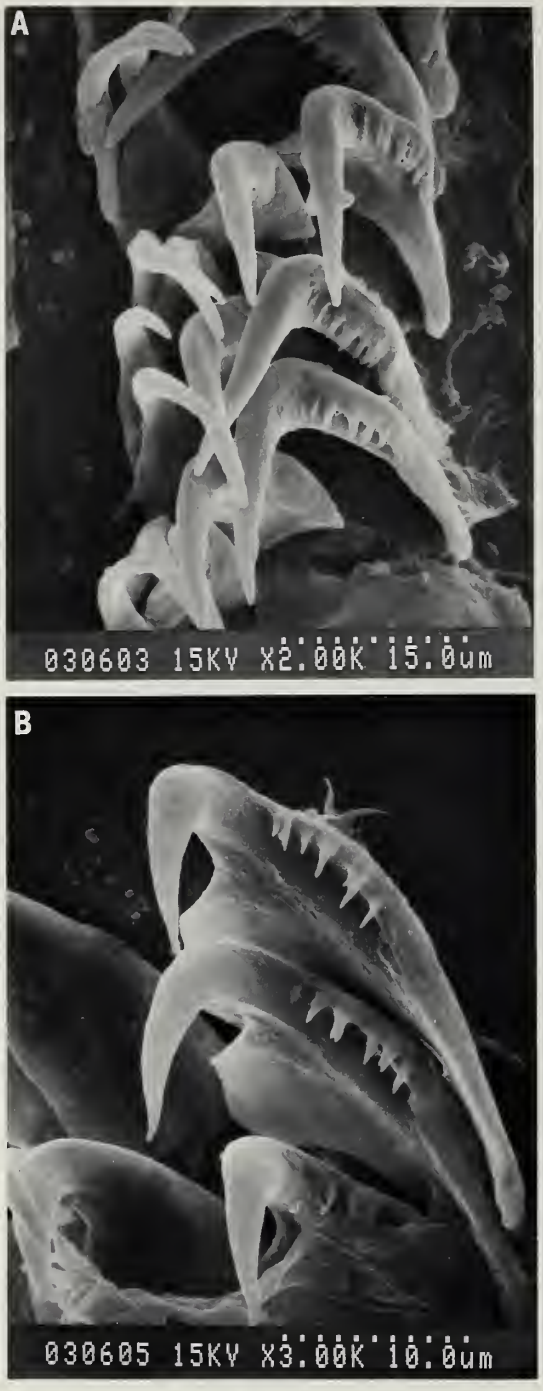

Figure 9

Siphopteron *brunneomarginatum* (Carlson & Hoff, 1974). Scanning electron micrographs A. Half-row of radular teeth. B. Inner lateral teeth.

Distribution: This species is known only from the type locality, Guam (Carlson & Hoff, 1974).

Material: Two specimens, California Academy of Sciences, San Francisco, CASIZ 066759, Bile Bay, Merizo, Guam, 11 December 1988, C. H. Carlson and P. J. Hoff.

External morphology: The two living animals were 4.0 mm in length. In aspects of their external morphology, they are identical to the original description.

Digestive system: The buccal mass is small and muscular. A pair of short, convoluted salivary glands is present on either side of the esophagus. Within the buccal mass is a thin chitinous cuticle, which is devoid of distinct jaw platelets. The radula is situated posteriorly. Its formula in one specimen is 21 × 3·1·0·1·3. The inner lateral teeth (Figure 11A) are broad with an elongate, curved primary cusp. A single small triangular denticle is present near the outer margin of the masticatory margin. The outer lateral teeth (Figure 11B) are simple and hook-shaped. They become progressively smaller towards the outer margins.

Central nervous system: The arrangement of ganglia (Figure 10A) is euthyneurous, with a short visceral loop. The paired cerebral ganglia are large and spherical. They are closely appressed, without a distinct commissure separating them. A distinct ganglionic mass is present dorsal to either cerebral ganglion. The pedal ganglia are situated ventral to the cerebral ganglia, and are joined to them by short connectives. The pedal ganglia are joined to each other by an elongate connective. Posterior to the left cerebral ganglion is the small left pleural ganglion. It is also joined to the left pedal ganglion by a short connective. Immediately posterior to the left pleural ganglion is the subintestinal ganglion. A short distance behind the subintestinal ganglion is the visceral ganglion. From it extends the visceral loop, which curves to the right and anteriorly. On the right side of the body the visceral loop joins the posterior end of the largely fused supraintestinal and right pleural ganglia.

Reproductive system: The arrangement of organs (Figure 10B) is monaulic. The ampulla is thick, with three or four convolutions. It narrows into the hermaphroditic duct, which passes under the albumen gland and curves again between the albumen and membrane glands. At this point a small pyriform receptaculum seminis joins the duct. The duct curves again and joins the genital aperture at the junction of the duct of the bursa copulatrix and the nidamental glands. The bursa is thin-walled and spherical. From the genital aperture, the ciliated sperm groove transports endogenous sperm to the penis, situated on the right side of the head.

The penis (Figure 10C) is similar to that of other members of the genus. The prostate is distinctly bifid in both specimens examined. Immediately anterior to the junction of the two prostatic lobes is the division into the penial

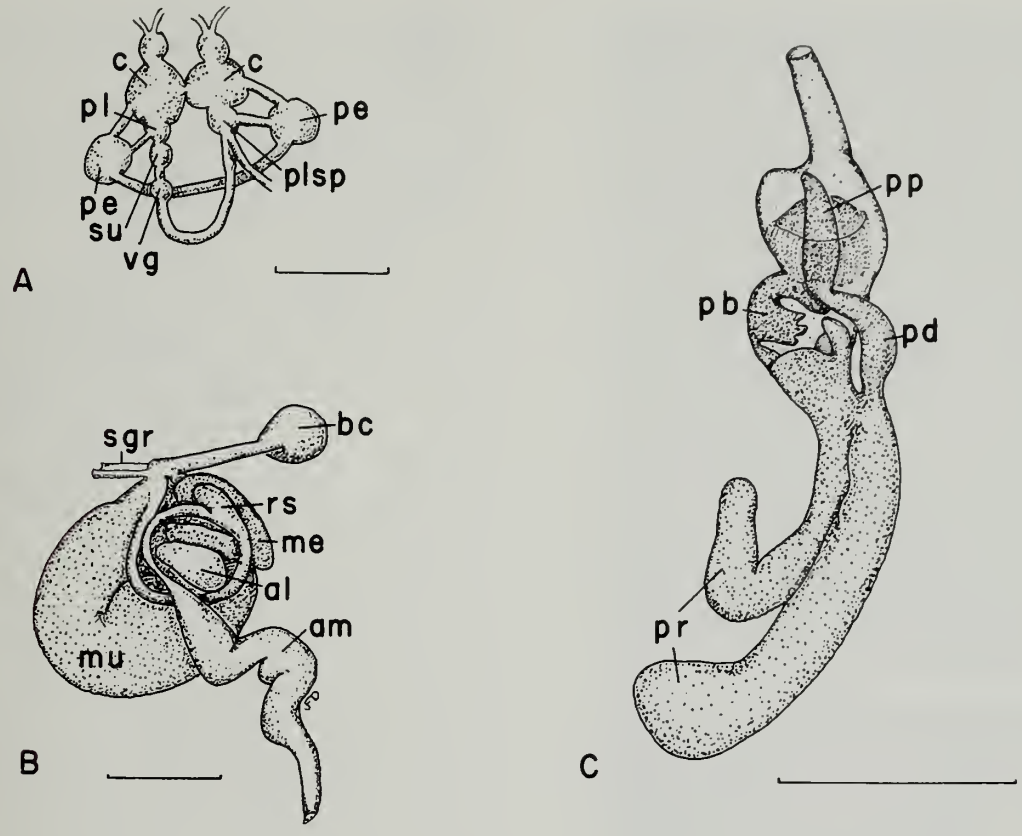

Figure 10

Siphopteron citrinum (Carlson & Hoff, 1974). A. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglion; pe, pedal ganglion; pl, pleural ganglion; plsp, fused pleural and supraintestinal ganglia; su, subintestinal ganglion; vg, visceral ganglion. B. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. C. Penis, scale = 0.5 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate.

bulb and penial duct. The penial bulb contains several muscular lobes. These lobes do not bear any rows of chitinous hooks, but do appear to have a few triangular lobes that may be enveloped by a chitinous lining. The penial duct is short and thick. At its anterior end is a short conical penial papilla that is surrounded by a cuplike layer of tissue within the penial sac. The penial papilla extends anteriorly, beyond the level of the tissue cup.

Discussion: The relationships of this species to ***Siphopteron*** *brunneomarginatum* and to ***S. nigromarginatum*** are discussed following the descriptive sections of these taxa.

Siphopteron nigromarginatum Gosliner, sp. nov.

(Figures 1C, 12, 13)

Distribution: This species is known only from the region surrounding Madang, Papua New Guinea.

Type material: Holotype, CASIZ 066562, SE side of Pig Island, Madang, Papua New Guinea, 10 m depth, 23 January 1988, T. M. Gosliner. One paratype, CASIZ 066565, dissected, Anemone Reef, Madang, Papua New Guinea, 3 m depth, 17 January 1988, T. M. Gosliner. One paratype, CASIZ 066563, SE side of Pig Island, Madang, Papua New Guinea, 10–12 m depth, 23 January 1988, T. M. Gosliner. One paratype, CASIZ 066564, dissected, SE side of Pig Island, Madang, Papua New Guinea, 23 January 1988, R. C. Willan. One paratype, CASIZ 066566, Planet Rock, 10 km S of Madang, Papua New Guinea, 10 m depth, 28 January 1988, T. M. Gosliner. One paratype, CASIZ 066567, dissected, Barracuda Point, Madang, Papua New Guinea, 9 m depth, 30 January 1988, T. M. Gosliner. Two paratypes, CASIZ 066568, Barracuda Point, 10–11 m depth, 7 and 8 February 1988, John Mizeu, T. M. Gosliner. One paratype, CASIZ 066569, The Quarry, 30 km N of Madang, Papua

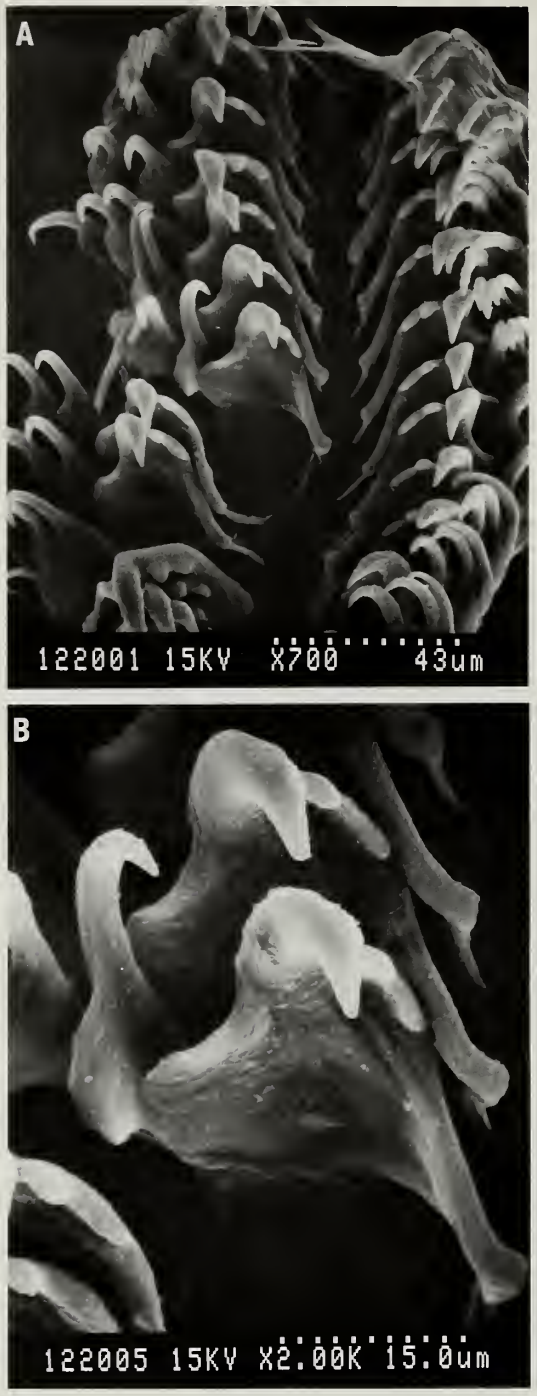

Figure 11

***Siphopteron** citrinum* (Carlson & Hoff, 1974). Scanning electron micrographs. A. Radular teeth. B. Inner lateral tooth.

New Guinea, 3 m depth, 12 February 1988, T. M. Gosliner. Two paratypes, CASIZ 066579, dissected, Anemone Reef and Rasch Pass, Madang, Papua New Guinea, 4–12 m depth, 14 and 15 February 1988, T. M. Gosliner.

Etymology: The epithet ***nigromarginatum*** refers to the black pigment that ornaments the siphonal and parapodial margins of this species.

Natural history: Specimens of ***Siphopteron nigromarginatum*** have been found under stones and crawling about in the open on shallow-water reef flats and slopes. A single specimen of this species was observed swimming in the laboratory.

External morphology: The living animals (Figures 1C, 12A) were 3–4 mm in length. The general body color is pale yellowish white to lemon yellow. Scattered orange mottlings may be present on the head shield and visceral hump. An area of opaque white is generally present at the base of the head shield, just anterior to the beginning of the visceral hump. Black pigment adorns the apex of the siphon, the tip of the siphonal crest, the parapodial margin, and the flagellum and its base. In one specimen, black pigment was absent from the flagellum.

The head shield is roughly triangular, broadest anteriorly. Posteriorly, it attenuates to an involuted siphon, which bears a prominent medial crest with an apical papilla elevated above the remainder of the siphon. The parapodia are elongate and widest near their anterior end, never overlapping, leaving most of the visceral hump exposed. Posteriorly, the parapodia extend as low ridges almost to the posterior end of the foot. The visceral hump is ovoid, broadest posteriorly. Anterodorsal of the posterior end of the visceral hump and to the right of the midline is an elongate, conical flagellum. In the holotype, the flagellum is bifurcate, whereas in the remainder of specimens it is uniramous. The gill is situated at the base of the ridge that terminates as the flagellum. It consists of 3 or 4 simply plicate lamellae. A distinct ridge extends from the anterodorsal surface of the ctenidium to the base of the flagellum. The foot is elongate, narrowest posteriorly. A large pedal gland is present in its posterior portion.

Digestive system: The buccal mass is elongate and weakly muscular. At the anteroventral end of the buccal mass is a large ventral oral gland. The esophagus is narrow and expands into a thin, saccate crop. At the junction of the esophagus with the posterior end of the buccal mass is a pair of thin, cylindrical salivary glands. Within the buccal mass there are no distinctly thickened jaws. The radular formula is 17–18 × 3·1·0·1·3 (Figure 13A) in three specimens examined. The inner lateral teeth (Figure 13C, D) are broad with a strong inner limb and an expanded outer lobe. Each inner lateral has a simply hooked cusp; a masticatory margin may bear a single triangular denticle on the outer end, adjacent to the central cusp (Figure 13D), and a series of 5–18 small, irregular denticles on its inner side. The large triangular denticle appears to be a result of the fusion of several smaller denticles (Figure 13C). The outer laterals (Figure 13B) are simply hook-shaped without any denticles. They possess a broad base and decrease in size towards the outer edges of the radula.

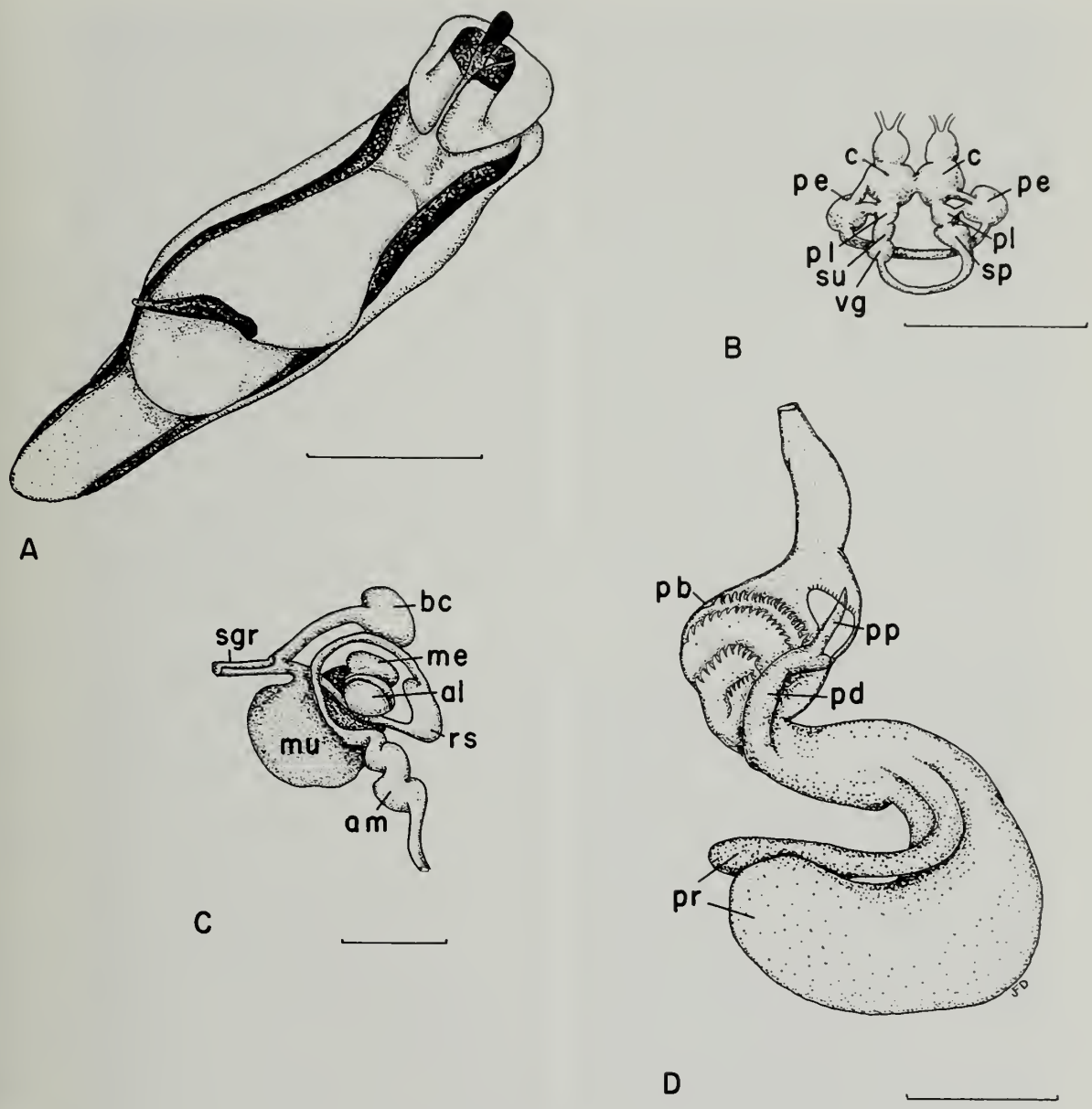

Figure 12

Siphopteron nigromarginatum Gosliner, sp. nov. A. Living animal, scale = 1.0 mm. B. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglion; pe, pedal ganglia; pl, pleural ganglia; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 0.5 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. D. Penis, scale = 0.25 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate.

Central nervous system (Figure 12B): As in other members of the family, the arrangement of ganglia is euthyneurous with a short visceral loop. The cerebral ganglia are large, without a distinct commissure separating them. Each ganglion possesses a large anterodorsal ganglionic mass that is only slightly smaller than the ganglion proper. Lateral and ventral to the cerebral ganglia are the large pedal ganglia. The pedal ganglia also connect with the small pleural ganglia, and are joined to each other by an elongate commissure. Posterior to the left pleural ganglion are the subintestinal and visceral ganglia. The visceral loop extends posteriorly from the visceral ganglion, curves

around the buccal mass, and joins the posterior portion of the supraintestinal ganglion.

Reproductive system (Figure 12C): The ampulla is narrow and convoluted. Distally from the ovotestis, it narrows into the hermaphroditic duct and curves around the large lobate mucous gland. The duct passes between the smaller albumen and membrane glands and joins the saccate receptaculum seminis. From there it continues to the hermaphroditic gonopore, where it joins the nidamental glands and the bursa copulatrix. The bursa is spherical and situated at the end of an elongate, narrow duct. From the gonopore, a ciliated sperm groove conducts spermatozoa to the cephalic penis.

The penis (Figure 12D) is elongate with a single or bilobed prostate. In three specimens the prostate was bilobed, whereas in two others it was undivided. The inner prostatic lobe, when present, is one-quarter to one-half as thick as the outer one. They may be joined for their anterior third or may be separate for almost their entire length. At the anterior end of the prostate is the bifurcation into the muscular bulb and the penial duct. The muscular bulb contains four distinct rows of chitinous spines. From posterior to anterior, there are 6, 10, 15, and 15 spines per row, respectively, in one specimen examined. The anterior end of the penial duct narrows into an elongate pointed apex that appears to be a chitinous stylet, which enters a flat papilla.

Discussion: The morphology of this species exhibits considerable variation. The coloration varies particularly in the amount of yellow and orange pigment present. Black pigment is present on the siphon, siphonal crest, and parapodial margins in all material examined, but was absent from the flagellum in one specimen. The flagellum is bifurcate in the holotype, but undivided in the remaining specimens. The elaboration of denticles on the inner lateral tooth exhibits various degrees of fusion in different specimens. The prostate may be single or bilobed.

Siphopteron nigromarginatum is similar in appearance to several other members of the genus with yellow or orange ground color ornamented with brown, black, or maroon pigment. Carlson & Hoff (1974) compared ***Siphopteron*** *citrinum, S. flavum,* and *S. brunneomarginatum.* They noted that *S. citrinum* is unique in having a single triangular denticle at the inner base of the central cusp of the inner lateral teeth and that it lacked any elongate denticles.

Subsequently, Gosliner (1984) described ***Siphopteron*** *flavobrunneum* and Gosliner & Williams (1988) described *S. michaeli,* which have similar coloration.

Despite the external similarity of these five taxa to each other and to ***Siphopteron nigromarginatum,*** several consistent external and internal differences clearly separate these species. ***Siphopteron*** *michaeli* and *S. flavobrunneum* both entirely lack a flagellum. In *S. flavum* the flagellum is a medial bulb at the posterior end of the visceral hump. In *S.* ***nigromarginatum,*** *S. brunneomarginatum,* and *S. citrinum,* the flagellum is elongate and situated well to the right of the medial line of the body. In *S. brunneomarginatum* the parapodia touch or overlap each other whereas in *S. citrinum* and *S.* ***nigromarginatum*** they are well separated. Swimming has been observed in *S. citrinum* and *S.* ***nigromarginatum,*** but not in *S. brunneomarginatum.* Most importantly, the penis of *S.* ***nigromarginatum*** bears several rows of chitinous spines, whereas *S. brunneomarginatum* and *S. citrinum* entirely lack penial spines.

In its external appearance, ***Siphopteron nigromarginatum*** is most similar to *S. citrinum.* In fact, specimens from Papua New Guinea were originally thought to be conspecific with *S. citrinum.* However, several consistent external and internal differences clearly distinguish the two species. Specimens of *S.* ***nigromarginatum*** always have black pigment on the margins of the parapodia and along the apical margin of the siphon. ***Siphopteron*** *citrinum* lacks black parapodial margins and black pigment is restricted to the apex of the siphonal crest, but is absent from the apical margins of the siphon. In both *S.* ***nigromarginatum*** and *S. citrinum* there is a distinct ridge from the dorsal surface of the gill to the flagellum.

The inner lateral teeth of ***Siphopteron*** *citrinum* have only a single denticle in addition to the elongate cusp, whereas in *S.* ***nigromarginatum*** there are more denticles. However, in the latter species these may exhibit some fusion of denticles to form triangular cusps.

In the central nervous system of ***Siphopteron nigromarginatum,*** the left pleural, subintestinal, and visceral ganglia are all appressed to each other, whereas in *S. citrinum* there is a gap between the subintestinal and visceral ganglia. In *S. citrinum* the supraintestinal and right pleural ganglia are largely fused, but in *S.* ***nigromarginatum*** they are distinct.

The most significant differences between the two species are in their penial morphology. In ***Siphopteron nigromarginatum*** distinct rows of chitinous spines line the penial bulb, whereas spines are entirely absent in *S. citrinum.* The penial papilla is thin and elongate in *S.* ***nigromarginatum*** and barely protrudes into a conical fleshy area. In *S. citrinum,* the papilla is short and fleshy, but extends well beyond a cuplike structure.

Based on these consistent differences within several organ systems, ***Siphopteron nigromarginatum*** and *S. citrinum* are considered as distinct species.

Siphopteron *pohnpei* (Hoff & Carlson, 1983)

(Figures 1D, 14, 15)

Gastropteron pohnpei Hoff & Carlson, 1983:261, figs. 1–3.
Siphopteron *pohnpei* (Hoff & Carlson, 1983) comb. nov.

Distribution: This species is known from Ponape and Palau (Hoff & Carlson, 1983) and Oahu, Hawaiian Islands (present study).

Material: One specimen, partially dissected, California

Figure 13

Siphopteron nigromarginatum Gosliner, sp. nov. Scanning electron micrographs. A. Entire radula. B. Half-row of radular teeth. C. Inner lateral tooth. D. Inner lateral tooth.

Academy of Sciences, San Francisco, CASIZ 066571, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 13 February 1986, 15 m depth, M. T. Ghiselin. One specimen, CASIZ 066572, dissected, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 13 February 1986, 15 m depth, T. M. Gosliner. Three specimens, CASIZ 066573, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 3 m depth, 10 September 1987, T. M. Gosliner. One specimen, CA-

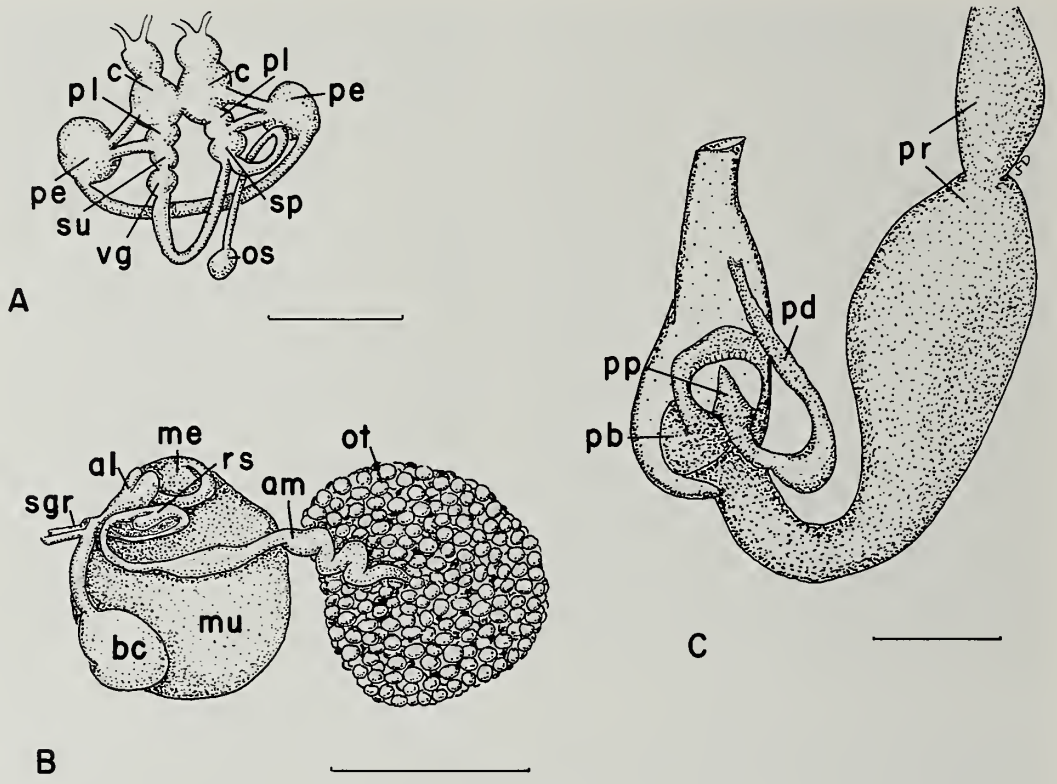

Figure 14

Siphopteron pohnpei (Hoff & Carlson, 1983). A. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglion; os, osphradial ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. B. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; ot, ovotestis; rs, receptaculum seminis; sgr, sperm groove. C. Penis with constricted prostate, scale = 0.1 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla.

SIZ 066574, dissected, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 3 m depth, 10 September 1987, T. M. Gosliner. Two specimens, both dissected, CASIZ 066575, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 10 September 1987, 3 m depth, T. M. Gosliner.

Natural history: Specimens have been found commonly inhabiting shallow subtidal sand flats in Kaneohe Bay, together with ***Siphopteron quadrispinosum*** sp. nov. The animals are capable of swimming by flapping their large parapodia.

External morphology: The living animals (Figure 1D) are 3–5 mm in length. The general body color is variable and ranges from brown to red. Brownish animals were observed to copulate with red ones. Animals with brown color may also have opaque white and yellow spots. Frequently, brown pigment is absent from the posterior end of the foot, leaving a translucent area on the posterodorsal portion of the animal. The head shield is short and triangular with an involuted siphon at its posterodorsal limit. The siphon contains a medial crest that terminates in an elongate, cylindrical extension. The visceral hump is elongate, ovoid with no flagellum or other elaboration in any of the observed specimens. The parapodia are well developed. The gill is situated on the right side of the body, ventral to a prominent crescentic ridge. It is minutely bipinnate, consisting of six primary leaflets.

Digestive system: The buccal mass is well developed and muscular. Anteroventral to the buccal mass is a prominent oral gland. At the junction of the esophagus with the posterior end of the buccal mass is a pair of large, ventrally reflexed salivary glands. No chitinous rodlets were observed on the jaws of the lining of the buccal mass. The radular formula was 17–19 × 4·1·0·1·4 in the two specimens observed. The inner lateral teeth (Figure 15C, D) are broad with an elongate central cusp. On the inner side of the cusp is a thick ridge bearing 8–10 elongate denticles. The outer laterals (Figure 15A, B) are also broad with a wing on their inner surface.

Central nervous system: The arrangement of ganglia (Figure 14A) is essentially identical to that described for

Figure 15

Siphopteron *pohnpei* (Hoff & Carlson, 1983). Scanning electron micrographs. A. Half-row of radular teeth of brown specimen. B. Half-row of radular teeth from red specimen. C. Inner lateral teeth of brown specimen. D. Inner lateral teeth of red specimen.

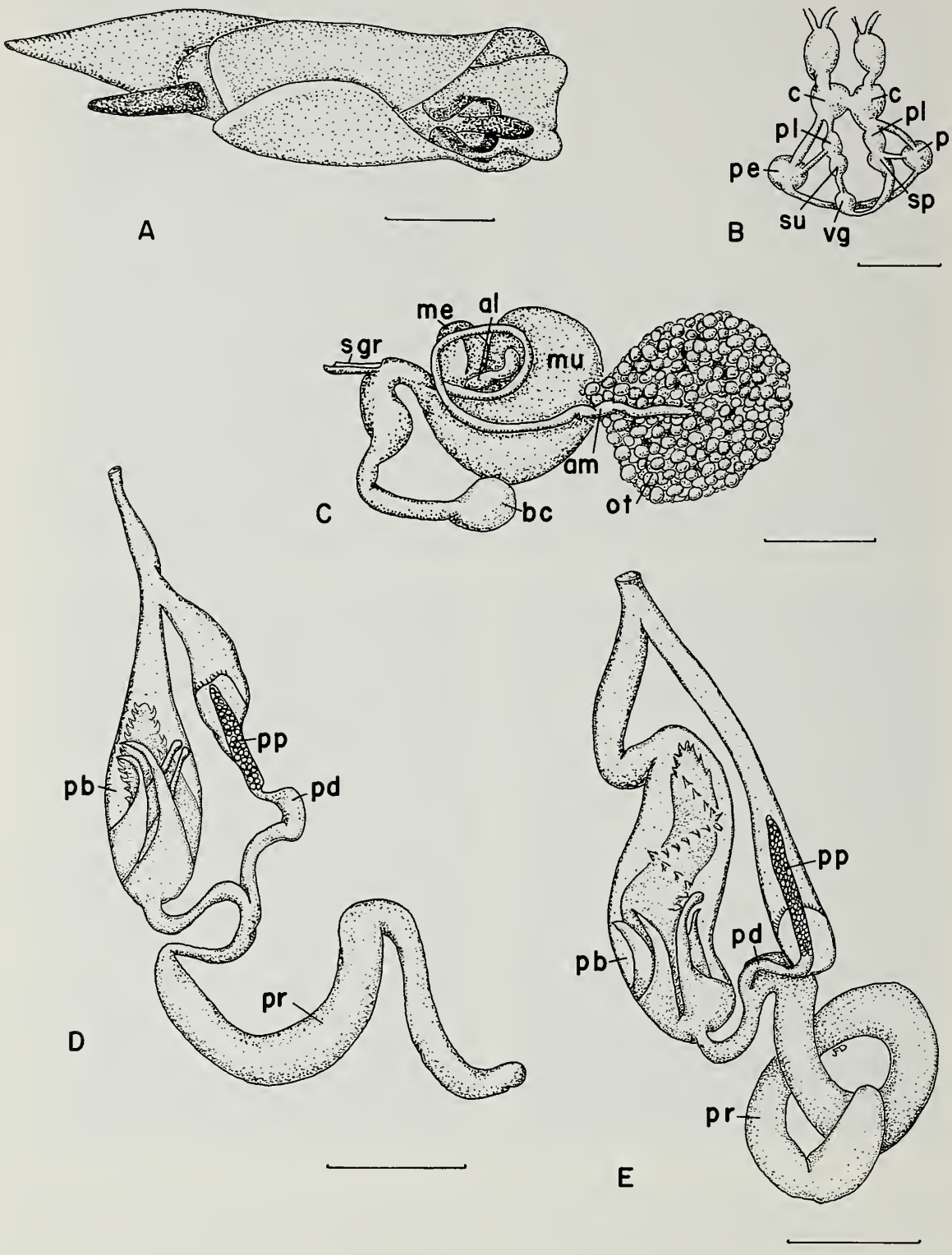

Figure 16

Siphopteron quadrispinosum Gosliner, sp. nov. A. Dorsal view of living animal, scale = 1.0 mm. B. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 0.5 mm. Key: al, albumen

Siphopteron *brunneomarginatum* above. The only exception is that a distinct osphradial ganglion was observed in *S. pohnpei*, and that its pedal ganglia appear larger than the cerebral ganglia.

Reproductive system: The organs are arranged in a monaulic fashion (Figure 14B). The ovotestis consists of numerous acini, arranged in a discoidal fashion. From the ovotestis a narrow preampullary duct expands into a highly convoluted ampulla. Distally, the ampulla narrows into the hermaphroditic duct. The hermaphroditic duct recurves near the basal portion of the albumen gland and expands and contracts again immediately proximal to the short, bulbous receptaculum seminis. More distally, the hermaphroditic duct again curves and joins the genital aperture together with the albumen, membrane, and mucous glands and the duct of the spherical bursa copulatrix. There is no separate duct from the hermaphroditic duct to the female glands, other than at the genital atrium. From the atrium, the ciliated sperm groove conducts endogenous sperm to the penis situated in the head.

The penis (Figure 14C) is complex in structure. In two specimens (one brown and one red) the proximal portion of the prostate was distinctly constricted, whereas in another two it was not. The prostate narrows distally and joins the unarmed, muscular penial bulb. Distal to the penial bulb is the penial papilla. From its proximal end a narrow duct curves distally to the distal portion of the penial sac.

Egg mass: The egg mass of ***Siphopteron*** *pohnpei* is a small spherical structure containing approximately 100 small white eggs. There is a single egg per capsule.

Discussion: ***Siphopteron*** *pohnpei* is known only from its original description (Hoff & Carlson, 1983). The brown specimens from the present material closely resemble the original description. Initially, the brown and red specimens appeared to represent two distinct species. However, all aspects of the external and internal morphology are identical in both color phases. This, combined with the fact that both color forms copulate readily with each other, suggests that they are all members of a single, variable species.

The radular morphology is identical in the specimens from Ponape and Hawaii.

The morphology of the penis, as noted above, is similar to that of ***Siphopteron*** *brunneomarginatum* and *S. citrinum*.

The eggs, unlike those of other known members of the genus, are white rather than yellow.

Siphopteron quadrispinosum Gosliner, sp. nov.

(Figures 1E, 16, 17)

Distribution: This species has been found only in the Hawaiian Islands (from Hookena, Kona coast of Hawaii, Jeff Hamann, pers. comm.; from Molikini Crater off Lanai, Mike Severns and Pauline Fiene, pers. comm.; and from Kaneohe Bay on Oahu) and from Madang, Papua New Guinea.

Type material: Holotype, California Academy of Sciences, San Francisco, CASIZ 066576, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 3 m depth, 10 September 1987, T. M. Gosliner. Forty paratypes, CASIZ 066577, same locality and date as holotype, T. M. Gosliner and M. T. Ghiselin. One paratype, CASIZ 066578, dissected, same date and locality as holotype. One paratype, CASIZ 066579, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 2 m depth, 25 October 1986, T. M. Gosliner. One paratype, CASIZ 066580, Cement Mixer Reef, Madang, Papua New Guinea, 19 October 1986, 3 m depth, T. M. Gosliner. One paratype, CASIZ 066581, The Quarry, N of Madang, Papua New Guinea, 10 m depth, 11 February 1988, T. M. Gosliner.

Etymology: The epithet ***quadrispinosum*** refers to the four prominent chitinous spines in the penial bulb, which characterize this species.

Natural history: The living animals are found most commonly on sand flats from shallow water (2–3 m depth) to depths of 30 m. In Papua New Guinea, two specimens were collected on the undersides of dead coral heads. The animals are capable of swimming for prolonged periods of time (up to 5 minutes) by flapping their parapodia.

External morphology: The living animals (Figures 1E, 16A) are 3–5 mm in length. The general body color is bright yellow. The siphon and flagellum are red-orange. In the specimens from Papua New Guinea, the red-orange pigment continues from the siphon along the posterior margin of the head shield and from the flagellum as a transverse line on the dorsal surface of the visceral hump. Also, in the New Guinea specimens, much of the visceral hump is milky white, rather than being uniformly yellow. In the Hawaiian specimens, the parapodial margin is opaque white, whereas it is uniformly yellow in the New Guinea specimens.

The head shield (Figure 16A) is triangular, rounded anteriorly, and terminating posteriorly as an involuted

←

gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; ot, ovotestis; sgr, sperm groove. D. Penis of Hawaiian specimen, scale = 0.2 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate. E. Penis of Papua New Guinea specimen, scale = 0.2 mm. Key: lettering same as D.

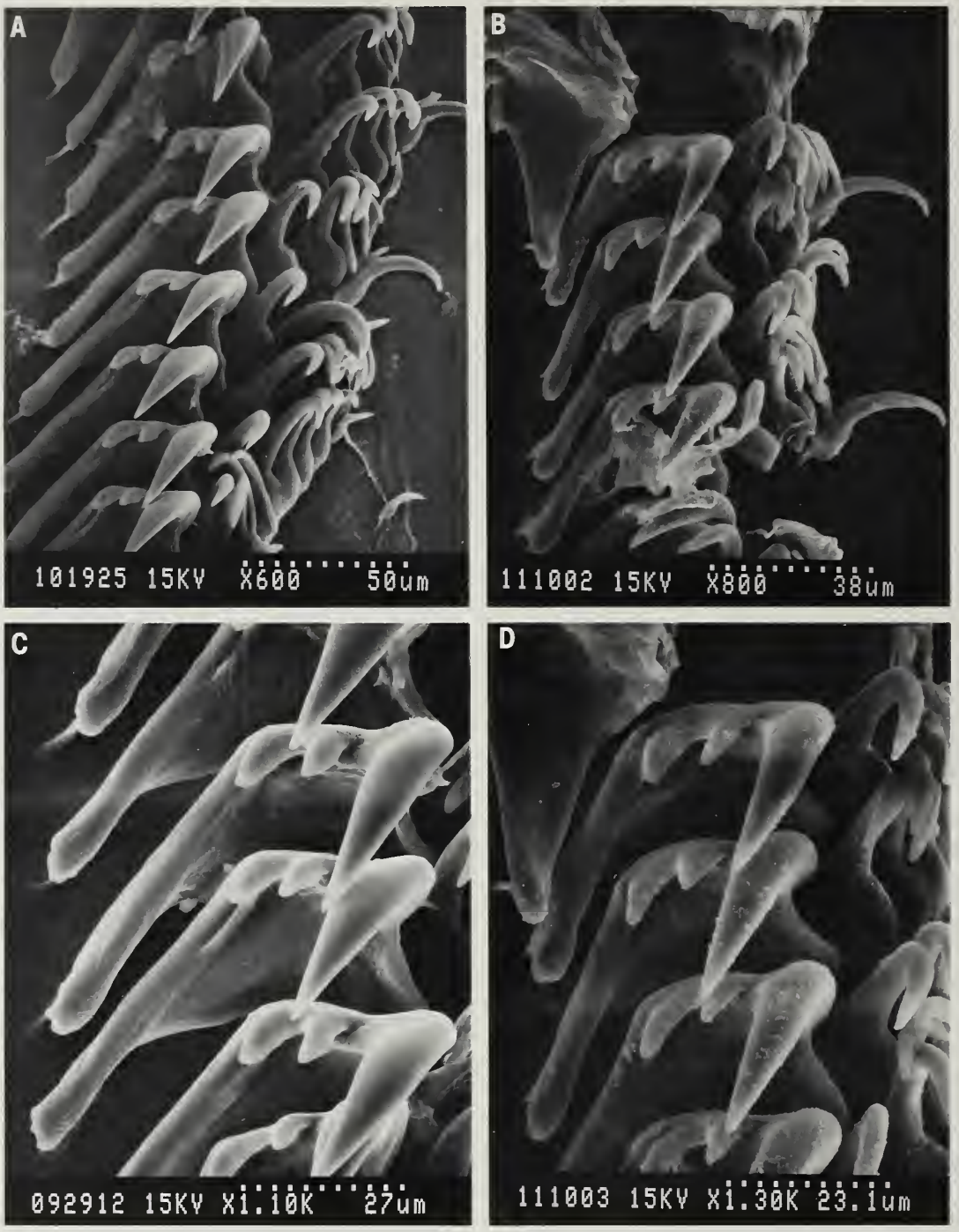

Figure 17

Siphopteron quadrispinosum Gosliner, sp. nov. Scanning electron micrographs. A. Half-row of radular teeth of Hawaiian specimen. B. Half-row of radular teeth of Papua New Guinea specimen. C. Inner lateral teeth of Hawaiian specimen. D. Inner lateral teeth of Papua New Guinea specimen.

siphon. The siphon has a prominent medial crest terminating in a papilla that extends above the level of the rest of the siphon. The visceral hump is elongate and ovoid with an elongate, acutely pointed posterior flagellum, situated just to the right of the midline. The parapodia are elongate and are sufficiently high that in resting animals the margins of the parapodia overlap. In preserved specimens it is possible to see numerous small glands along the outer third of the parapodia. The foot is elongate and actuely pointed posteriorly. A large ovoid pedal gland is present on the ventral surface of the foot. The gill, situated on the right side of the body, consists of 4–6 simple plicae.

Digestive system: The buccal mass is large and muscular. A small ventral oral gland is present at the anteroventral margin of the buccal mass. Paired, convoluted salivary glands are present at the junction of the esophagus with the posterior end of the buccal mass. Jaws bearing five or six rows of chitinous rodlets are contained within the anterior portion of the buccal mass. The radular formula in two specimens was 18–20 × 4–6·1·0·1·4–6. The inner lateral teeth (Figure 17C, D) are broad with an elongate cusp. A pair of triangular cusps is present on the inner masticatory margin. The outer lateral teeth (Figure 17A, B) are simple, hook-shaped, and without denticles. They decrease in size towards the outer margin.

Central nervous system: The arrangement of ganglia (Figure 16B) is virtually identical to that described for ***Siphopteron*** *brunneomarginatum*.

Reproductive system: The arrangement of organs (Figure 16C) is monaulic. The large, discoidal ovotestis consist of numerous acini. The preampullary duct is narrow and does not expand dramatically as it becomes the slightly convoluted ampulla. The ampulla narrows as it becomes the hermaphroditic duct and wraps around the albumen and membrane glands. A distinct receptaculum appears to be absent. The hermaphroditic duct curves distally between the membrane, albumen, and mucous glands and joins the widened genital atrium. The spherical bursa copulatrix has a narrow duct, which triples its width in the ectal third of its length.

The structure of the complex penis (Figure 16D, E) was examined in three specimens. The prostate is elongate with two or three major convolutions. Distally, it narrows for a variable portion of its length. Prior to its junction with the penial bulb, a narrow duct emerges and runs to the penial papilla. There is an elongate and reticulate spine in the penial papilla. The apex of the fleshy portion is rounded and ciliated. Within the penial bulb are four large, gold chitinous spines. The apices of two of these are capitate and the other two are acutely curved. More distally, there is a fleshy papilla, which is ornamented with a row of spines on either margin. There are 11 or 12 spines on the inner side and 3 or 4 spines on the outer side in the two Hawaiian animals examined. In the specimen from Papua New Guinea, there are two rows of spirally arranged spines with 12 spines on the inner side and 19 on the outer one. The spiral arrangement is likely due to partial contraction of the papilla. The penial bulb and penial papilla join near the distal end of the penial aperture.

Egg mass: The egg mass is spherical with numerous yellow, individually encapsulated eggs.

Discussion: The external and internal morphology of the animals from the Hawaiian Islands is remarkably consistent in the greater than fifty specimens observed. The specimens from Papua New Guinea differ from the Hawaiian animals in several small aspects of their color and in the arrangement of penial spines. The fact that they are similar in radular morphology and in the remainder of the detailed structure of the penis suggests that they are indeed conspecific. Examination of more material from the western Pacific is required to ensure that this is a single widespread species rather than a species pair.

The radular morphology, with a pair of triangular denticles on the inner surface of the inner lateral tooth, is similar to that found in *Sagaminopteron* Tokioka & Baba, 1964 (Tokioka & Baba, 1964; Carlson & Hoff, 1973, 1974; present study). However, species of *Sagaminopteron* can be distinguished from members of ***Siphopteron*** by the presence of a large bipinnate or tripinnate ctenidium, broader, more numerous outer lateral teeth, and simple penis. The fact that ***Siphopteron quadrispinosum*** has a separate duct leading to a distinct penial papilla confirms that it is more closely allied to other Indo-Pacific species of ***Siphopteron*** than to *Sagaminopteron*.

Siphopteron quadrispinosum can be distinguished from all other Gastropteridae by its yellow body color with red-orange siphon and flagellum. It is the only species of ***Siphopteron*** known to possess consistently a pair of triangular denticles on the inner margin of the inner lateral tooth. Some specimens of ***S. nigromarginatum*** appear to have two triangular denticles, but the scanning electron microscope reveals that these are fusions of small denticles. Its penial morphology, with three different sets of cuticular spines, is unique among known members of the Gastropteridae.

Siphopteron tigrinum Gosliner, sp. nov.

(Figures 1F, 18–20)

Distribution: This species is known from Palau (Clay Carlson and Patty Jo Hoff, pers. comm.), Queensland, Australia (Richard Willan, pers. comm.), Tulear, Madagascar (present study), and Papua New Guinea (present study).

Type material: Holotype, California Academy of Sciences, San Francisco, CASIZ 064343, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 20 October

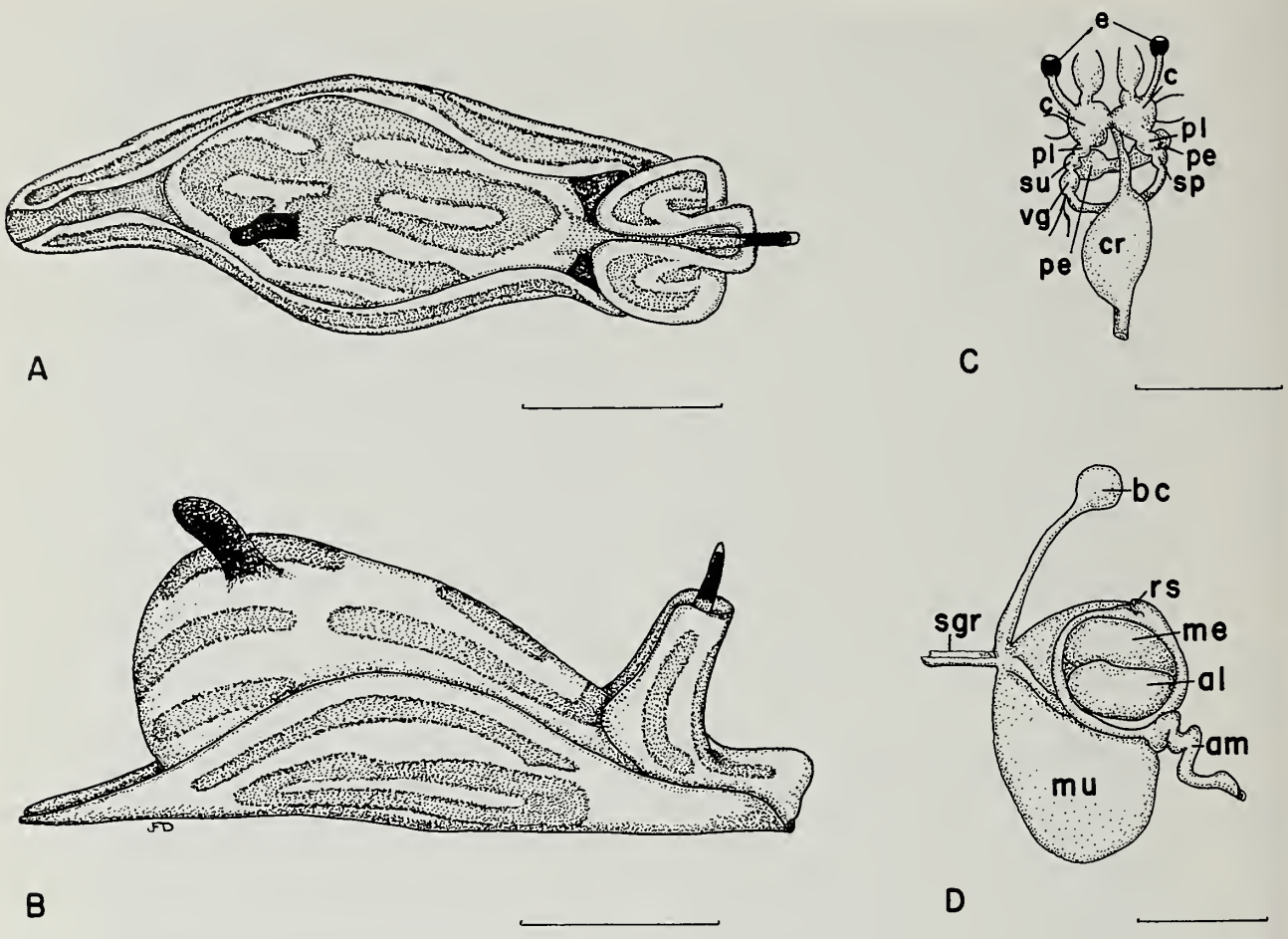

Figure 18

Siphopteron tigrinum Gosliner sp. nov. A. Dorsal view of predominately blue living animal, scale = 1.0 mm. B. Lateral view of predominantly orange living animal, scale = 1.0 mm. C. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglion; cr, crop; e, eye; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. D. Reproductive system, scale = 0.5 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove.

1986, T. M. Gosliner. Two paratypes, CASIZ 064344, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 20 October 1986, T. M. Gosliner. One paratype, CASIZ 066582, dissected, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 20 October 1986, T. M. Gosliner. One paratype, CASIZ 066345, dissected, Cement Mixer Reef, Madang, Papua New Guinea, 3 m depth, 22 October 1986, T. M. Gosliner. Paratype, one specimen, Sek Passage, Madang, Papua New Guinea, 27 October 1986, Michael T. Ghiselin. Two paratypes, CASIZ 066583, Barracuda Point, Madang, Papua New Guinea, 10 m depth, 8 February 1988, J. Mizeu. Four paratypes, CASIZ 066584, SE side of Pig Island, Madang, Papua New Guinea, 10 m depth, 23 and 24 January 1988, T. M. Gosliner. One paratype, CASIZ 066585, Rempi Lagoon, N of Madang, Papua New Guinea, 6 m depth, 3 February 1988, T. M. Gosliner. Two paratypes, CASIZ 066586, The Pinnacle, Madang, Papua New Guinea, 10 m depth, 25 January 1988, T. M. Gosliner. One paratype, CASIZ 066587, The Chimney, Madang, Papua New Guinea, 17 m depth, 30 January 1988, G. Williamson. One paratype, CASIZ 066588, N side Kranket Island, Madang, Papua New Guinea, 10 m depth, 24 January 1988, T. M. Gosliner. One paratype, CASIZ 066589, S side of Rasch Passage, Madang, Papua New Guinea, 8 m depth, 14 February 1988, R. C. Willian. Two paratypes, CASIZ 066590, Sek Passage, Madang, Papua New Guinea, 11 m depth, 21 February 1988, T. M. Gosliner. One paratype, CASIZ 066591, Madang Light, Madang, Papua New Guinea, 12 m depth, 1 February 1988, T.

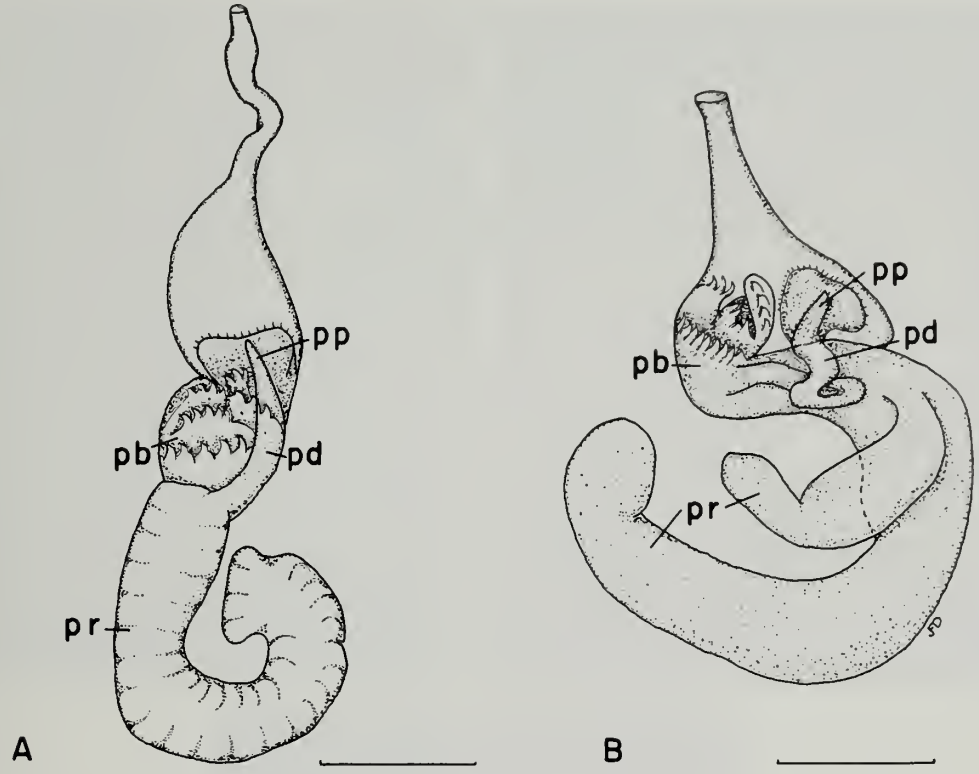

Figure 19

Siphopteron tigrinum Gosliner, sp. nov. A. Penis with undivided prostate, scale = 0.2 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate. B. Penis with bilobed prostate, scale = 0.2 mm. Key: Lettering as in A.

M. Gosliner. One paratype, CASIZ 066592, Sek Passage, Madang, Papua New Guinea, 9 m depth, 1 February 1988, T. M. Gosliner.

Etymology: The epithet ***tigrinum*** refers to the striped pattern of coloration, resembling that of a tiger.

Natural history: Specimens have been found commonly on the under surface of coral rubble, on shallow reefs. It is the most abundant species of gastropterid in Madang, Papua New Guinea, where it has been found together with ***Siphopteron nigromarginatum, Siphopteron*** *brunneomarginatum*, ***Siphopteron quadrispinosum***, and *Sagaminopteron psychedelicum*. This species has never been observed to swim.

External morphology: The living animals (Figures 1F, 18A, B) are 3–4 mm in length. The ground color is brilliant orange. The head shield, visceral hump, and outer surfaces of the parapodia possess narrow, elongate blue patches, surrounded by a narrow line of purplish blue. On the dorsal surface of the foot a yellowish triangular patch is present. The apex of the siphon, at the posterior end of the head shield, and the entire length of the posterior flagellum are black.

The head shield is short, roughly triangular. The posterior end of the shield is involuted, forming a distinct siphon. A prominent medial crest within the siphon terminates in an elevated papilla. The visceral hump is rounded posteriorly. Near its posterior end, on the right half of the body, is an elongate, conical flagellum. The parapodia are elongate, reaching the middle of the visceral hump in height. They are not distinctly separated from the foot. Posteriorly, the foot is elongate and triangular. The ventral surface of the foot contains an elongate pedal gland near its posterior limit. On the right side of the visceral hump is the simply plicate ctenidium, consisting of 3 or 4 leaflets.

Digestive system: The muscular buccal mass is short and bulbous. A large oral gland is present ventral to the buccal mass. Within the buccal mass is a thin cuticular lining, devoid of any jaw rodlets. The radular formula is 20 × 3·1·0·1·3 in two specimens examined. The inner lateral teeth (Figure 20C) are broad with an elongate curved cusp. On the inner side of the tooth is a short masticatory margin, which may bear up to eight irregular denticles or may be entirely smooth. The outer lateral teeth (Figure 20A, B) have a short triangular base and an elongate curved cusp. The width of the base of the teeth decreases towards the

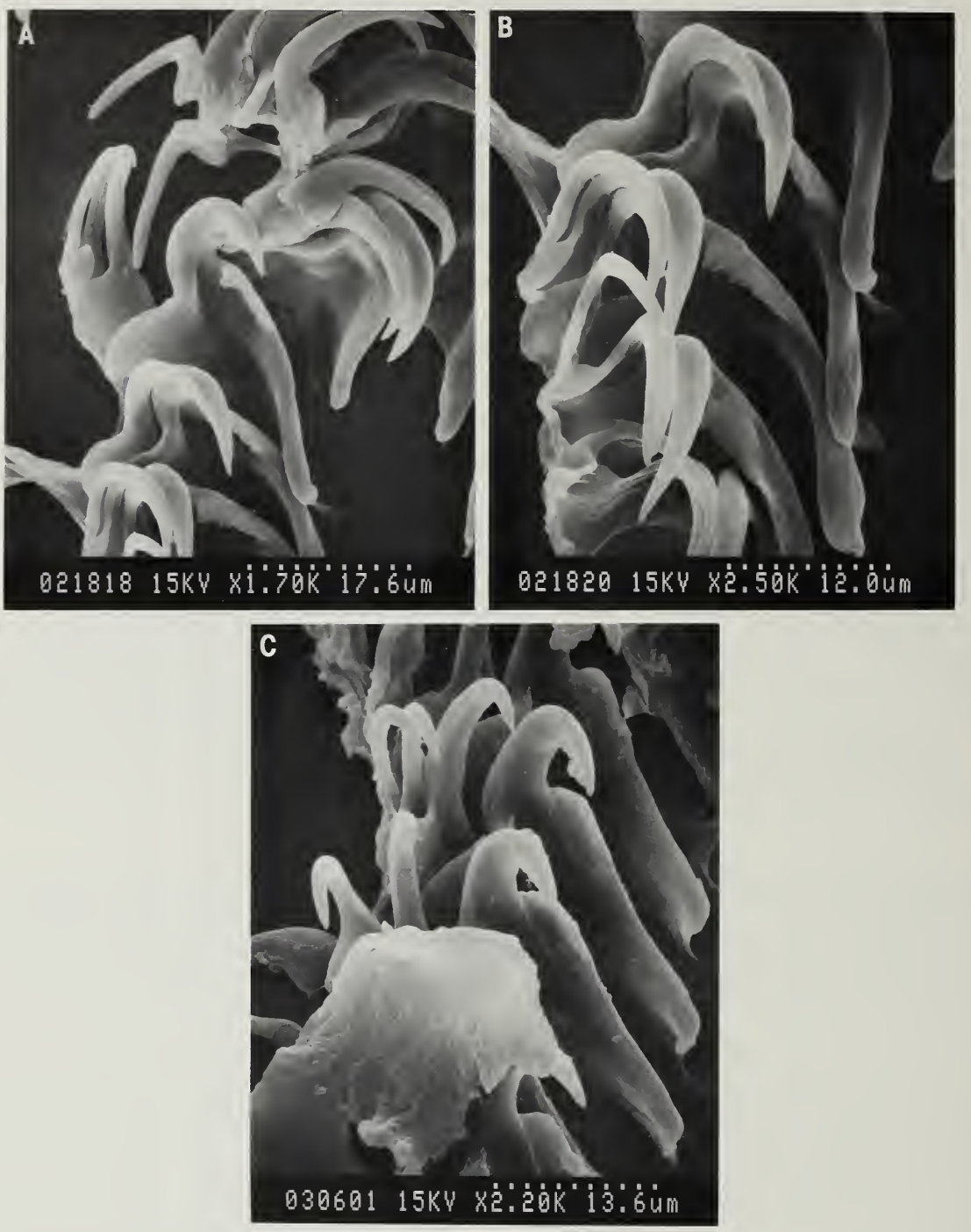

Figure 20

Siphopteron tigrinum Gosliner, sp. nov. Scanning electron micrographs. A. Half-row of radular teeth. B. Half-row of radular teeth. C. Inner lateral teeth.

outer margin of the radula. No denticles are on the outer laterals.

Extending from the posterior end of the buccal mass is a short narrow esophagus. At the juncture of the esophagus with the buccal mass is a pair of large salivary glands. The esophagus expands into a bulbous thin-walled crop.

Central nervous system (Figure 18C): All of the ganglia of the euthyneurous nervous system are situated within the circumesophageal nerve ring. The large cerebral ganglia are appressed to each other, without a distinct commissure. Extending dorsally from the cerebral ganglia are thickenings of nervous tissue, which are almost as large as the ganglia. Adjacent to these thickenings are the optic nerves, with a large eye at each apex. The pedal ganglia are slightly smaller than the cerebrals and are ventral to them. They are separated by a commissure, the length of which is approximately equal to the diameter of the pedal ganglion. Immediately posterior to the right cerebral ganglion is the right pleural ganglion. The supraintestinal ganglion is directly posterior to the right pleural. From its posterior end emerges the visceral nerve. The visceral nerve forms a short loop and, on the left side, joins the visceral ganglion adjacent to two other prominent nerves. The subintestinal ganglion is situated between the visceral and left pleural ganglia.

Reproductive system (Figure 18D): The arrangement of reproductive organs is monaulic. The ampulla is narrow and convoluted. It narrows further into the hermaphroditic duct, which encircles the albumen and membrane glands. A short sessile receptaculum seminis is situated near the outer edge of the female gland mass, near the middle of the hermaphroditic duct. The hermaphroditic duct terminates at the common gonopore, near the junction of the large mucous gland and the duct of the bursa copulatrix. The bursa is spherical and thin-walled. From the common genital opening, the ciliated sperm groove extends anteriorly to the penial aperture on the right side of the head.

The penis is large and is situated on the right and posterior sides of the buccal mass. In one specimen (Figure 19A) the prostate is thick and curved, consisting of a single lobe. In the second specimen (Figure 19B) there are two distinct prostatic lobes. The prostate enters a muscular vestibule that contains four areas of chitinous hooks. The posteriormost is a single straight row of 6–9 hooks, in the two specimens examined. Anteriorly there may be two or three rows of hooks which are embedded in large muscular flaps. There are 3–5 hooks on each of these flaps. In one specimen, an additional anterior row of seven hooks is present. From the juncture of the prostate and the vestibule a narrow duct runs anteriorly and enters the penial papilla in the penial sac proper. The papilla is broadest anteriorly and ciliated on its outer edge.

Discussion: ***Siphopteron tigrinum*** is immediately distinguishable from other members of the Gastropteridae by its unique coloration. No other member of the family has orange coloration with blue, purple, and black ornamentation. It is similar to *S. citrinum* (Carlson & Hoff, 1974), ***S. nigromarginatum***, *S. fuscum* (Baba & Tokioka, 1965), *S. ladrones* (Carlson & Hoff, 1974), and ***S. quadrispinosum*** sp. nov. in that it has an elongate flagellum on the right side of the body. A flagellum may be present or absent in *S. brunneomarginatum* (Carlson & Hoff, 1974) (Gosliner & Williams, 1988; present study).

The radular morphology is similar to that of ***Siphopteron*** *ladrones* (Carlson & Hoff, 1974; Gosliner, 1988a), *S. brunneomarginatum* (Carlson & Hoff, 1974; present study) and *S. michaeli* (Gosliner & Williams, 1988) in that the denticles of the inner lateral tooth, when present, are few in number and weakly developed. In both *S.* ***tigrinum*** and *S. michaeli*, denticles may be present or entirely absent from the masticatory margin of the inner lateral teeth.

The penial morphology of ***Siphopteron tigrinum*** is most similar to that of ***S. nigromarginatum*** (present study), *S. michaeli* (Gosliner & Williams, 1988:fig. 2D), and *S. flavum* (Tokioka & Baba, 1964) (present study). In all four of these species, a muscular vestibule is situated between the prostate and penial sac, which bears several transverse rows of recurved chitinous hooks. Also, a separate duct leads from the junction of the prostate and the vestibule leading to the penial papilla. The penial morphology of ***S. tigrinum*** is also similar to that of *S. michaeli*, ***S. nigromarginatum***, and *S. brunneomarginatum* in that members of both species may have either an undivided or bilobed prostate in different individuals.

Despite the similarities in radular and penial morphology, ***Siphopteron tigrinum*** and *S. michaeli* can be readily distinguished. The two differ markedly in their coloration. In ***S. tigrinum*** there are bright blue and purple lines, whereas *S. michaeli* has large maroon spots. ***Siphopteron*** *michaeli* entirely lacks a flagellum. The right pleural and supraintestinal ganglia are distinct in ***S. tigrinum***, whereas they are fused in *S. michaeli*.

Siphopteron *flavum* (Tokioka & Baba, 1964)

(Figures 21, 22)

Gastropteron flavum Tokioka & Baba, 1964:212, figs. 5–7, pl. 10, figs. 10–12; pl. 11, figs. 6–8; pl. 13, fig. 3; Baba & Tokioka, 1965:374, fig. 7D; Carlson & Hoff, 1974: 346, figs. 12E, 13A; Bertsch & Johnson, 1981:18, 19, unnumbered figure.

Siphopteron *flavum* (Tokioka & Baba, 1964) comb. nov.

Distribution: This species is known from Japan (Tokioka & Baba, 1964; Baba & Tokioka, 1965), Guam (Carlson & Hoff, 1974), and the Hawaiian Islands (Bertsch & Johnson, 1981).

Material: Four specimens, dissected, California Academy of Sciences, San Francisco, CASIZ 066593, Bile Bay, Merizo, Guam, 6 m depth, 29 February and 16 April, 1976,

Figure 21

Siphopteron flavum (Tokioka & Baba, 1964). Scanning electron micrographs. A. Half-row of radular teeth. B. Inner lateral teeth of specimen from Guam. C. Half-row of radular teeth of specimen from Hawaii.

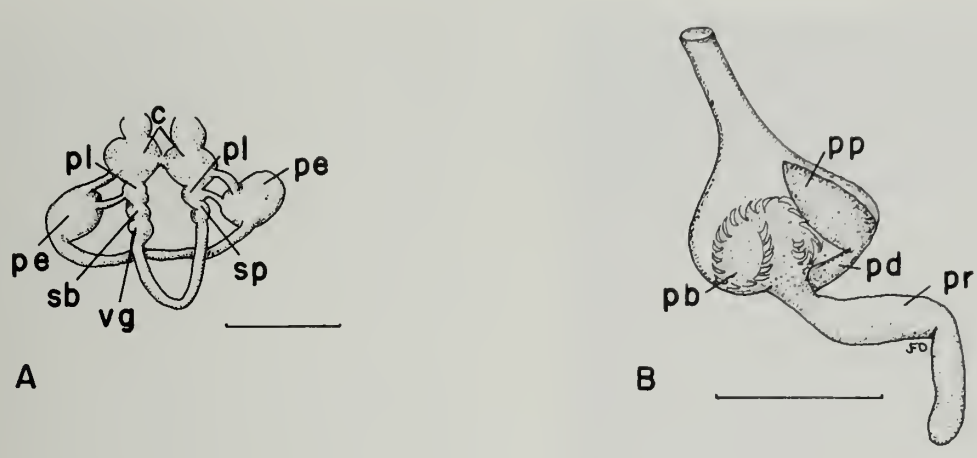

Figure 22

Siphopteron flavum (Tokioka & Baba, 1964). A. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglia; pe, pedal ganglion; pl, pleural ganglia; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. B. Penis, scale = 0.25 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate.

Clay Carlson and Patty Jo Hoff. One specimen, CASIZ 066594, 16 m depth, Maui, Hawaiian Islands, December 1988, Pauline Fiene.

External morphology: The living animals were 2–4 mm in length. Their general morphology agrees entirely with that described previously (Tokioka & Baba, 1964; Baba & Tokioka, 1965; Carlson & Hoff, 1974).

Digestive system: The buccal mass is small and highly muscular. Within its anterior portion is a chitinous cuticle, devoid of distinct jaw plates. The radular formula in one 4-mm specimen was 18 × 3·1·0·1·3. The inner lateral teeth (Figure 21A, B) are large and broad, with a prominent, curved primary cusp. The masticatory border bears 12 or 13 irregular, triangular denticles. The outer lateral teeth (Figure 21A) are simply hook-shaped, without denticles, and decrease in size towards the outer margins of the radula.

Central nervous system: The arrangement of ganglia (Figure 22A) is virtually identical to other members of ***Siphopteron*** described here. The large cerebral ganglia are appressed to each other without a distinct commissure. They give rise to anterodorsal ganglionic thickenings. The large pedal ganglia are joined to the cerebral and pleural ganglia by short, paired commissures, and to each other by an elongate connective. Posterior to the left pleural ganglion are the subintestinal and visceral ganglia. A short visceral loop joins the visceral ganglion to the supraintestinal ganglion, which is appressed to the right pleural ganglion.

Reproductive system: Details of posterior reproductive organs could not be discerned, owing to poor preservation. The penis (Figure 22B) is similar to other members of ***Siphopteron*** described in this paper. The prostate is short with a single convolution. At its anterior end, the prostate gives rise to the penial bulb and the duct of the penial papilla. The penial bulb contains a central fleshy lobe armed with 24 radially arranged hooks. A smaller lateral lobe bears five additional curved spines. The penial duct is short and narrow. It expands into a simple, conical penial papilla that is devoid of armature. The penial papilla and penial bulb merge into the anterior penial sac, which then joins the ciliated sperm groove at the right anterior extreme of the head.

Discussion: ***Siphopteron flavum*** is morphologically similar to other members of the genus. It is unique in that it possesses a terminal rather than lateral flagellum and has penial bulb spines arranged in a large circular whorl with a smaller lateral row of spines.

Gastropteron bicornutum Baba & Tokioka, 1965

(Figures 1G, 23, 24)

Gastropteron bicornutum Baba & Tokioka, 1965:364, text figs. 1–6, pl. 25, figs. 1–9; Baba, 1970:figs. 3–5.

Distribution: This species is known only from Japan (Baba & Tokioka, 1965) and Papua New Guinea (present study).

Material: Two specimens, California Academy of Sciences, San Francisco, CASIZ 066595, W side of Tabat Island, Madang, Papua New Guinea, 10 m depth, on coarse sandy slope, among *Halophila*, 9 February 1988, T. M. Gosliner. One specimen, CASIZ 066596, W side of Pig Island, Madang, Papua New Guinea, 10 m depth, on coarse sandy slope among *Halophila*, 15 February 1988, T. M. Gosliner. One specimen, CASIZ 066597, dissected, W side of Pig Island, Madang, Papua New Guinea, 10 m depth, on coarse sand slope among *Halophila*, 15 February 1988, T. M. Gosliner.

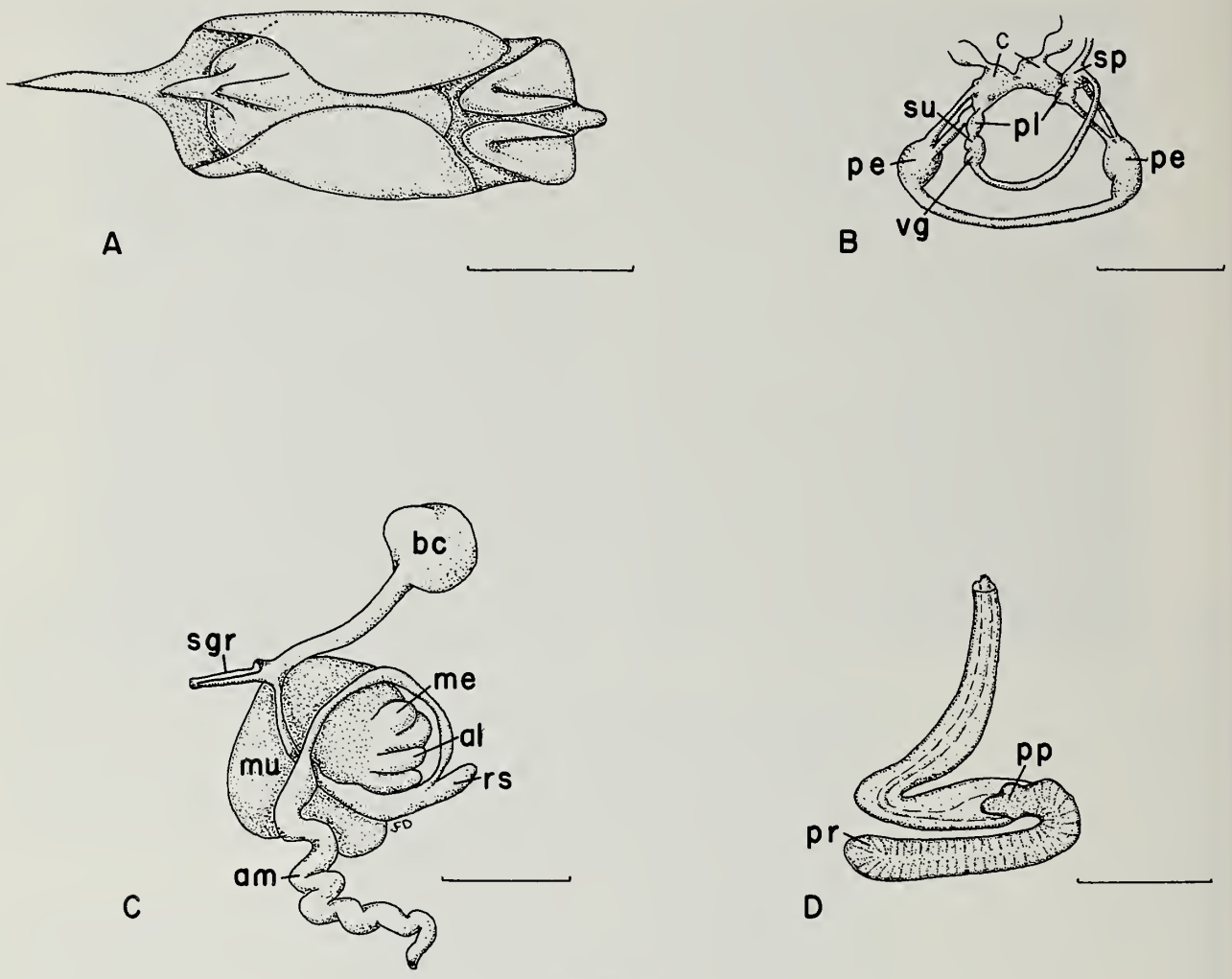

Figure 23

Gastropteron bicornutum Baba & Tokioka, 1965. A. Dorsal view of living animal, scale = 2.0 mm. B. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglia; os, osphradial ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. D. Penis, scale = 0.5 mm. Key: pp, penial papilla; pr, prostate.

Natural history: All four specimens studied here were found near the sea grass, *Halophila* sp., on shallow subtidal sandy slopes. This species closely resembles both an undescribed *Chelidonura* sp. and an undescribed haminoeid, with which it is sympatric. Gosliner & Behrens (1989) have suggested that these three taxa form a Müllerian mimicry complex.

External morphology: The four living specimens (Figures 1G, 23A) were 5–7 mm in length. The general body color is translucent white. Black, opaque white, and yellow-orange pigment spots are scattered over the surface of the body in variable densities. This variable pattern makes the animal appear mottled gray or black, depending on the relative densities of white and black pigments. The head shield (Figure 23A) is broad and triangular. Posteriorly, it terminates in an involuted siphon, which lacks a central ridge. The large and well developed parapodia enable *Gastropteron bicornutum* to swim for extended periods of time. The posterior ends of the parapodia extend just posterior to the hind end of the visceral hump. The visceral hump is oval with a large conical flagellum situated at its posteromedial end. Immediately dorsal to this flagellum is a second, slightly more elongate flagellar process. The ctenidium is large, consisting of 13 primary filaments. The foot is wide for most of its length. Anteriorly, it is bilobed and posteriorly it is tapered with a narrow, elongate "tail." Ventrally, a large pedal gland is present at the posterior end of the foot.

Digestive system: Ventral to the large muscular buccal mass is a large oral gland. At the junction of the esophagus with the posterior end of the buccal mass is a pair of large, ventrally directed salivary glands. Within the anterior portion of the buccal mass is a pair of well-developed jaws. These jaws contain numerous, rodlike elements. The radular formula is 20 × 4·1·0·1·4 in one specimen examined. The broad inner lateral teeth bear 8–11 elongate denticles on the masticatory margin (Figure 24). The outer laterals are narrow and hook-shaped, with a prominent swelling near their bases.

Central nervous system (Figure 23B): The large cerebral ganglia are appressed, with a short commissure separating them. A large swelling of nervous tissue is present at the anterodorsal portion of either cerebral ganglion. Ventral to the cerebral ganglia are the slightly larger pedal ganglia, which are separated from each other by an elongate commissure. Extending posterior from each cerebral ganglia, and joining with the pedal ganglia, is a smaller pleural ganglion. Immediately posterior to the left pleural ganglion, and partially fused with it, is the subintestinal ganglion, followed immediately by the larger visceral ganglion. The visceral loop extends around the posterior portion of the buccal mass, curves anteriorly, and joins the supraintestinal ganglion adjacent to the osphradial nerve. The supraintestinal ganglion is situated immediately dorsal to the right pleural ganglion.

Reproductive system (Figure 23C): The reproductive anatomy of *Gastropteron bicornutum* is virtually identical to that described for *Sagaminopteron psychedelicum,* with the exception that the shape and relative sizes of the nidamental glands differ slightly. Also, the bursa copulatrix of *G. bicornutum* is more spherical.

The penis (Figure 23D) contains a simple, curved prostate, a short, unarmed, conical papilla, and an elongate duct leading to junction of the penis with the sperm groove.

Discussion: *Gastropteron bicornutum* was originally described from eight preserved specimens (Baba & Tokioka, 1965). Subsequently, Baba (1970) described the living animal and morphology of the penis. The present material from Papua New Guinea agrees with the previous descriptions in virtually all respects. The specimen described here has a small, but distinct penial papilla, not illustrated by Baba.

Figure 24

Gastropteron bicornutum Baba & Tokioka, 1965. Scanning electron micrograph of half-row of radular teeth.

Gastropteron ***chacmol*** Gosliner, sp. nov.

(Figures 1I, 25, 26)

Gastropteron rubrum: Marcus & Marcus, 1960: *non rubrum* (Rafinesque, 1814); Gosliner & Armes, 1984, in part: 60, figs. 19–22, *non rubrum* (Rafinesque, 1814).

Distribution: This species was collected from the Yucatan Peninsula of Mexico. Specimens probably attributable to this species have also been collected from Key Biscayne, Florida, Grand Cayman Island (Marcus & Marcus, 1960; Gosliner & Armes, 1984, as *Gastropteron rubrum,* see following discussion), and Caracas Island, Venezuela (Jeff Hamann, pers. comm.).

Type material: Holotype, CASIZ 066598, in front of Hotel La Ceiba, Puerto Morelos, Quintana Roo, Mexico, 8 m depth, in mixed sand and *Thalassia,* 4 April 1985, T. M. Gosliner. Twenty-three paratypes, CASIZ 066599, same date and locality as holotype, T. M. Gosliner and M. T. Ghiselin. One paratype, CASIZ 059658, with shell removed, in front of La Ceiba Hotel, Puerto Morelos, Quintana Roo, Mexico, 3 m depth, 27 March 1985, M. T. Ghiselin.

Natural history: Specimens of this species have been collected commonly in mixed coarse sand where turtle grass (*Thalassia testudinum* Banks *ex* Konig) and a variety of green algae predominate. The animals are competent swimmers and may propel themselves through the water column for extended periods of time.

Etymology: A "chacmol" is a reclining figure that is present in several Mayan sites on the Yucatan Peninsula. It is believed that a chacmol served as an altar for offerings of human organs. This species is named after a chacmol because of its geographical proximity to these statues and because of its blood red color.

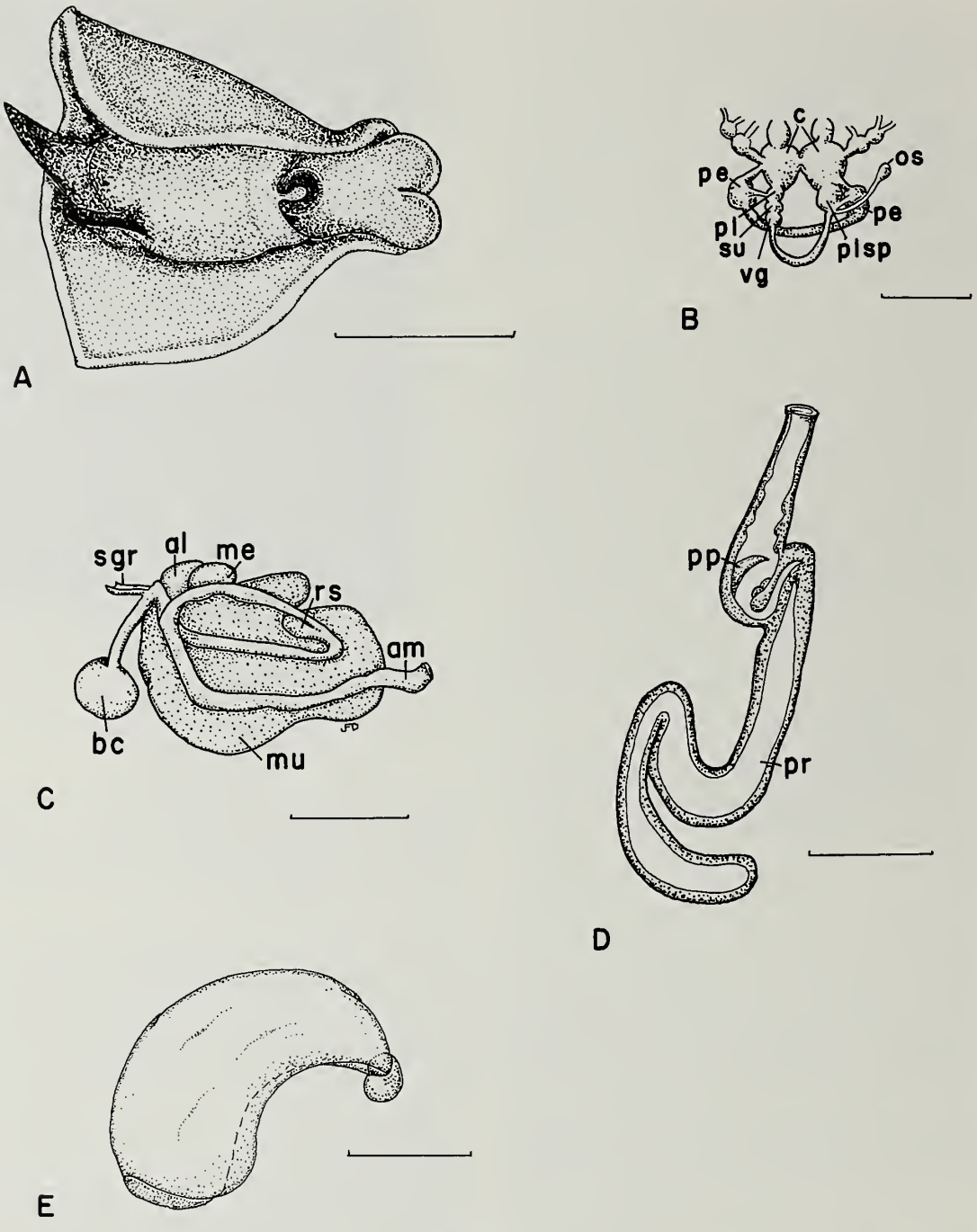

Figure 25

Gastropteron ***chacmol*** Gosliner, sp. nov. A. Living animal, scale = 2.0 mm. B. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglia; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 0.5 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. D. Penis, scale = 0.5 mm. Key: pr, prostate. E. Shell, scale = 0.5 mm.

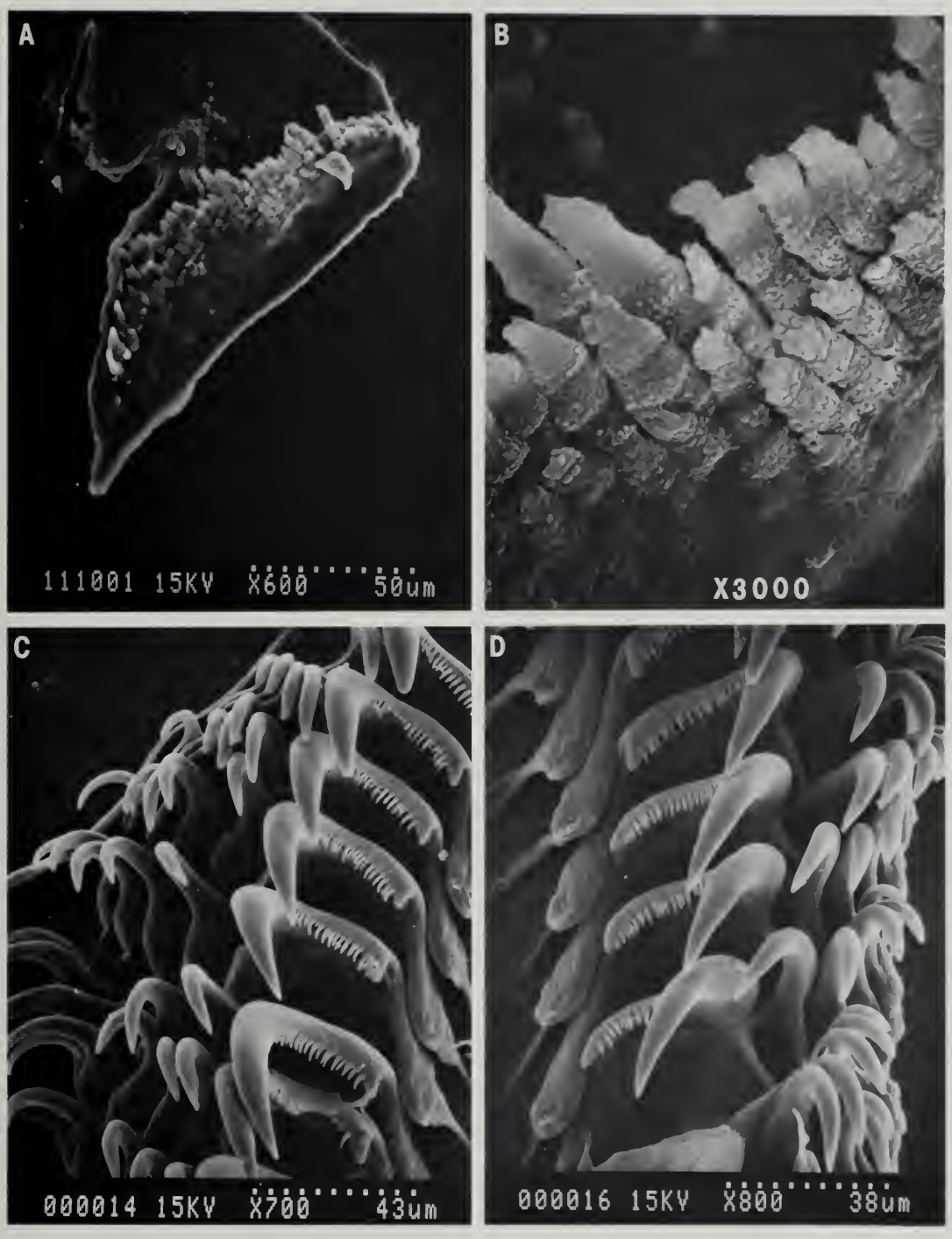

Figure 26

Gastropteron ***chacmol*** Gosliner, sp. nov. Scanning electron micrographs. A. Entire jaw. B. Jaw elements. C. Half-row of radular teeth. D. Half-row of radular teeth.

External morphology: The living animals (Figures 1I, 25A) are 3–7 mm in length. The general body color is deep red to plum. Minute yellow spots are scattered over the surface of the body in some specimens. The parapodial margin is bright yellow. The head shield is rounded and bilobed anteriorly, with a deeply emarginate medial cleft. The head shield tapers posteriorly into an involuted siphonal margin, which lacks a distinct medial crest. The

visceral hump is elongate and ovoid. An elongate filiform flagellum is present on the right side of the body, between the gill and posterior end of the visceral hump. The parapodia are elongate and high, overlapping each other when the animal is at rest. The parapodia are joined to the rest of the body anteriorly and are free for most of their length. There is no distinct separation between the foot and parapodia. The large gill, consisting of 7–10 distinct, simply plicate leaflets, is situated on the right side of the body. A large, ovoid pedal gland is present within the posterior portion of the foot.

Shell: The morphology of the shell was studied in one specimen. It consists of a small, calcified embryonic portion and a larger membranous, conchiolin wing (Figure 25E).

Digestive system: The buccal mass is large and muscular. A large oral gland is present ventral to the anteriormost portion of the buccal mass. A pair of moderately elongate salivary glands extends posteriorly from the junction of the esophagus with the posterior end of the buccal mass. The anterior end of the buccal mass contains a pair of chitinous jaws (Figure 26A) which are composed of numerous, finely papillate rodlets (Figure 26B). The radular formula is 17–19 × 5·1·0·1·5 in three specimens examined. The inner lateral teeth (Figure 26C, D) are broad with a sharp elongate cusp. On the inner margin of the inner lateral teeth is an elongate masticatory margin, bearing 21–24 small, elongate denticles. The edentate outer lateral teeth are progressively shorter and narrower towards the outer margins.

Central nervous system: The arrangement of ganglia (Figure 25B) is euthyneurous with a short visceral loop. The large cerebral ganglia are appressed to each other, without a distinct commissure. From their anterior surface arises a slightly smaller concentration of nervous tissue. Laterally and ventrally there are also several swellings and branchings of cerebral nerves. Ventral to the cerebral ganglia are the slightly smaller pedal ganglia, which are connected to each other by a short commissure. Immediately posterior to the left cerebral ganglion are the left pleural, subintestinal, and visceral ganglia. Extending posteriorly from the right cerebral ganglion are the right pleural and supraintestinal ganglia. From the posterior end of the supraintestinal ganglion arise the visceral and osphradial nerves. The visceral nerve joins the visceral ganglion on the other side of the body. The osphradial nerve leads to a small osphradial ganglion.

Reproductive system: The arrangement of reproductive organs is monaulic (Figure 25C). The ampulla is straight and narrow. There is no distinct division between the ampulla and the hermaphroditic duct. The hermaphroditic duct passes over the surface of the mucous gland and loops around the albumen and membrane glands. Just before curving back to the genital aperature is a small swelling, the short receptaculum seminis. The hermaphroditic duct joins the genital aperture at the junction of the nidamental glands and the bursa copulatrix. The thin-walled bursa is connected to the genital aperture by a short stalk.

The penis (Figure 25D) has a thick prostrate with a single convolution. The penis occupies much of the anterior portion of the body. The prostate narrows distally and emerges into the penial sac. The penial sac lacks a distinct papilla but contains a proximally directed, fleshy lobe that is lined by chitin. The penial aperture joins the anterior end of the sperm groove on the right side of the head.

Egg mass: The egg mass is a gelatinous sphere that is attached to the substrate by means of a mucus thread. Within this gelatinous mass are numerous individually encapsulated yellow eggs.

Discussion: *Gastropteron* ***chacmol*** most closely resembles *G. rubrum* (Rafinesque, 1814) and *G. vespertilium* Gosliner & Armes, 1984, in aspects of its coloration, external anatomy, and internal anatomy (Table 1). These three species have an elongate flagellum on the right side of the body and inner lateral teeth bearing numerous small denticles. All three species differ in their coloration. The ground color of *G. vespertilium* is grayish or purplish black with occasional blue-gray spots on the parapodia. Yellow, or more rarely green or blue, lines are present on the margins of the siphon and parapodia. The flagellum is translucent white. The ground color of *G. rubrum* is pale red with scattered white or yellow spots and pale yellow or bluish white lines on the parapodial and siphonal margins (Salvini-Plawen & Abbott, 1974; Malcolm Edmunds, pers. comm.). Though *G.* ***chacmol*** is also reddish in color, the red is deeper and richer, and the parapodial margin is a bright yellow. The siphon and flagellum are the same color as the ground color, without any additional pigment.

Gastropteron ***chacmol*** is most similar to *G. vestpertilium* in external morphology. Both are small in size (a maximum of 5–7 mm in length), have a distinctly bilobed anterior margin of the head, and have a gill composed of 10 or fewer leaflets. In contrast, *G. rubrum* is large (up to 30 mm in length), has an undivided head, and has a large gill composed of 23–30 leaflets.

Internally, differences also separate the three species. The radula in the three species is very similar in formula and shape and number of teeth. The radular teeth of *Gastropteron rubrum* are larger, but are thin and flimsy. The denticles on the masticatory margin of the inner lateral teeth are weakly developed.

The cerebral ganglia of *Gastropteron* ***chacmol*** are appressed to each other, without a distinct commissure, while both *G. rubrum* and *G. vespertilium* have a commissure that at least equals the diameter of the ganglia.

The most profound differences between *Gastropteron* ***chacmol***, *G. rubrum*, and *G. vespertilium* are in the structure of the penis. Both *G.* ***chacmol*** and *G. vespertilium* have a short, indistinct penial papilla, whereas that of *G. rubrum* is elongate and conical. The prostate of *G.* ***chacmol***

Table 1

Morphological variation in three *Gastropteron* species.

Species	Color	Length	Gills	Radula	Cerebral commissure	Penial papilla	Prostate
Gastropteron rubrum	pale reddish with white spots, white or yellow parapodial & siphonal lines	10–26 mm	23–30	20–40 × 5·1·0·1·5	present	elongate	highly convoluted
Gastropteron vespertilium	grayish black with blue-gray spots, yellow, blue, or green parapodial & siphonal lines	3–5 mm	9–10	15–21 × 5–6·1·0·1·5–6	present	short	1 convolution
Gastropteron ***chacmol***	deep red to plum, yellow or blue parapodial line	3–7 mm	7–11	16–19 × 5·1·0·1·5	absent	short	1 convolution

and *G. vespertilium* is thick, consisting of only one or two convolutions, whereas that of *G. rubrum* is thin and highly convoluted (Gosliner & Armes, 1984). In addition, *G. vespertilium* possesses a separate spermatic bulb, which is absent in the other two species.

In the description of *Gastropteron vespertilium*, Gosliner & Armes (1984) reviewed the morphology of *G. rubrum*, based on the pertinent literature and examination of Mediterranean and eastern and western Atlantic material. The western Atlantic specimens had fewer gill lamellae and were smaller in length. Differences between eastern and western Atlantic individuals were attributed to smaller size and immaturity of the western Atlantic material. However, the discovery of mature individuals of *G.* ***chacmol*** ranging from 3 to 7 mm has necessitated the re-examination and more critical comparison of specimens of *G. rubrum* studied by Gosliner and Armes. The holotype of *G. rubrum manx* Marcus & Marcus, 1966, from West Africa, together with specimens from Palermo, Italy, agrees completely with the description by Gosliner & Armes (1984:figs. 24, 25) and previous accounts of *G. rubrum* from the Mediterranean (Vayssière, 1880, 1885; Bergh, 1893; Guiart, 1901). On the other hand, the two western Atlantic specimens from Florida (USNM 836667) and Grand Cayman Island (CASIZ 034121) have a slightly convoluted prostate without an elongate penial papilla. The remainder of their morphology is identical to that of *G.* ***chacmol***. Therefore, all published records of *G. rubrum* in the western Atlantic likely refer to *G.* ***chacmol*** rather than to *G. rubrum*.

Gastropteron ***hamanni*** Gosliner, sp. nov.

(Figures 1H, 27, 28)

Distribution: This species is known only from the type locality in the Turks and Caicos Islands.

Type material: Holotype, CASIZ 066603, Sellars Cut, Provodenciales Island, Caicos Islands, Turks and Caicos, 20 m depth, Jeff Hamann.

Etymology: *Gastropteron* ***hamanni*** is named for Jeff Hamann, who collected the only known specimen of this species. Jeff is a good friend and has been an enthusiastic and generous supporter of opisthobranch research for many years.

External morphology: The living animal (Figure 1H) was 4 mm in length. The ground color is uniformly yellow with a maroon apex to the siphon. The head shield is roughly triangular, broadest anteriorly. It is relatively short, comprising only about one-fourth of the body length. Its posterior end forms an involuted siphon, which lacks a distinct medial crest. The parapodia are elongate and high, overlapping each other when the animal is actively crawling. The visceral hump is elongate and ovoid, without any flagellum or other appendages. The gill is small, consisting of 2 or 3 indistinct leaflets. The foot is not distinctly separated from the parapodia. A large pedal gland is present at the posterior end of the foot.

Digestive system: The buccal mass (Figure 27A) is short and muscular. A pair of large, ventrally directed salivary glands is present at the junction of the esophagus with the posterior end of the buccal mass. The salivary glands are two to three times the length of the buccal mass. Within the buccal mass is a thin, chitinous lining. No distinct jaws with rodlets were observed. A small radula was present. Its formula was 12 × 3·1·0·1·3. The inner lateral teeth (Figure 28A, B) are broadly triangular, narrow in the outer portion. There are approximately eight short, indistinct denticles on the sloping masticatory border. The outer lateral teeth are thin and simply hook-shaped, with only a single cusp.

Central nervous system: The arrangement of the ganglia (Figure 27B) is euthyneurous. The cerebral ganglia are large and appressed to each other, without a distinct commissure. The pedal ganglia are approximately the same size as the cerebrals and are connected to each other by an elongate commissure. Immediately posterior to the left

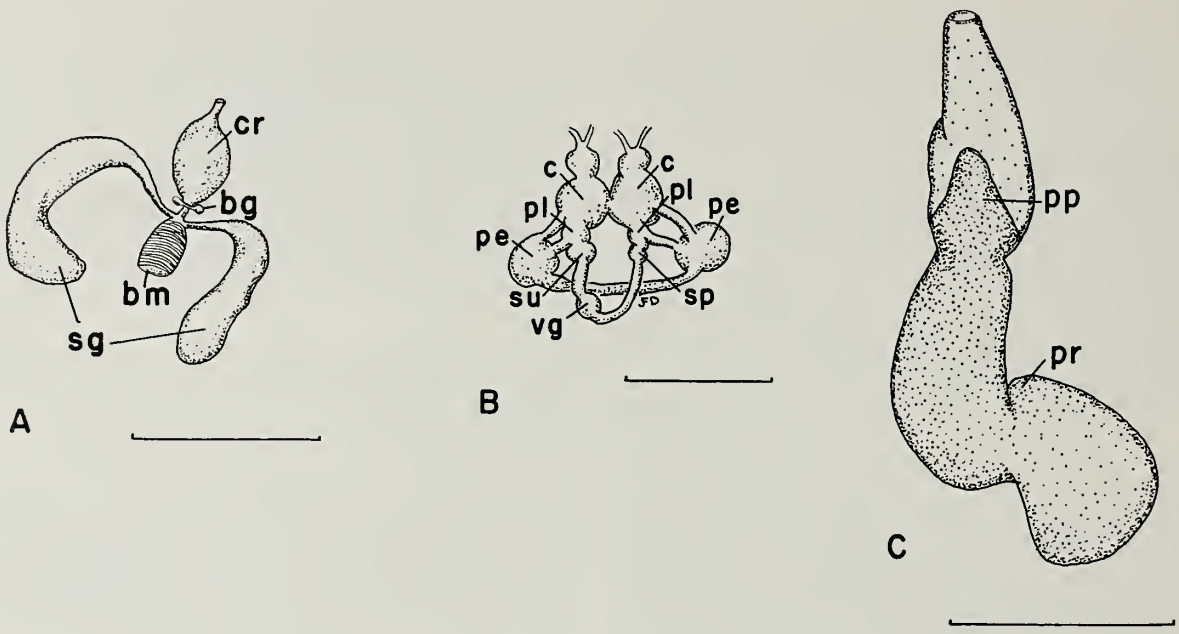

Figure 27

Gastropteron ***hamanni*** Gosliner, sp. nov. A. Buccal mass, scale = 1.0 mm. Key: bg, buccal ganglia; bm, buccal mass; cr, crop; sg, salivary gland. B. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Penis, scale = 0.2 mm. Key: pp, penial papilla; pr, prostate.

cerebral ganglion are the left pleural and subintestinal ganglia. After a moderate distance there is a small visceral ganglion. The visceral loop curves behind the esophagus and joins the supraintestinal ganglion on the right side of the body. Immediately anterior to the supraintestinal ganglion is the right pleural ganglion.

Reproductive system: Details of the posterior genital complex could not be ascertained owing to poor preservation. The penis (Figure 27C) is simple with a short, slightly curved prostate, which joins a short penial sac. No distinct papilla is in the sac.

Discussion: In its coloration *Gastropteron* ***hamanni*** most closely resembles ***Siphopteron*** *flavum* (Tokioka & Baba, 1964). However, G. ***hamanni*** lacks dark pigment on the posterior end of the visceral hump. It also lacks the medial siphonal crest and distinctive posterior extension of the visceral hump that characterize *S. flavum* (Tokioka & Baba, 1964; Carlson & Hoff, 1974; Bertsch & Johnson, 1981). The radular morphology of the two species appears similar except that *S. flavum* appears to have a more extensive masticatory margin than in *G. hamanni*.

The most significant differences between the two species are in the structure of the penis. *Gastropteron* ***hamanni*** has a simple unarmed penis, whereas ***Siphopteron*** *flavum* has a distinct penial bulb containing two series of curved hooks and a separate penial duct and papilla.

Gastropteron ***odhneri*** Gosliner, sp. nov.

(Figures 29, 30)

Distribution: This species is known only from the type locality, Bonin Island, Japan.

Type material: Holotype, Naturhistoriska Riksmuseet, Stockholm, Dr. Sixten Bocks' Japan Expedition 1914, off Chichijima, Bonin Islands (Ogasawara), Japan, 70 fathoms (ca. 128 m) depth, 8 July 1914, S. Bocks.

Paratypes, five specimens. Naturhistoriska Riksmuseet, Stockholm No. 1288, same locality and date as holotype.

Etymology: This species is named after the late Dr. Nils Hjalmar Odhner, who contributed greatly to our understanding of opisthobranch systematics and evolution. Dr. Odhner first indicated that these specimens represented an undescribed species.

External morphology: The preserved specimens (Figure 29A, B) are 4–5.5 mm in length. The head shield is bilobed anteromedially and is roughly triangular. There is no distinct siphonal crest at its posterior limit, only a short posterior lobe. The parapodia are broad, extending for most of the length of the animal. The visceral hump is ovoid. On its right side is a curved ridge that partially covers the ctenidium. At the posterior limit of the visceral hump is a curved, triangular flagellum. The ctenidium is composed

of 3–5 pinnate leaflets. The anus is situated immediately posterior to the gill. The foot (Figure 29B) is distinct from the parapodia and is widest posteriorly. An ovoid pedal gland is present in the posterior third of the foot. It has an elongate slit extending posteromedially from the glandular body to the posterior limit of the foot.

Shell: Although the shell was entirely dissolved in all material, a large curved conchiolin membrane remained, indicating that *Gastropteron* ***odhneri*** likely possesses a large, calcified shell.

Digestive system: The buccal mass is large and muscular, occupying much of the region of the head shield. At the junction of the esophagus with the posterodorsal end of the buccal mass is a pair of elongate, tubular salivary glands. The esophagus is elongate and glandular and joins the stomach within the large digestive gland. Numerous foraminiferans were contained within the stomach of one specimen. There is a large labial cuticle, bearing rows of distinct jaw platelets (Figure 30A), which are restricted to two small areas on the medial portion of its anterodorsal margin. The radular formula in one specimen was 23 × 6·1·0·1·6. The inner lateral teeth (Figure 30B, C) are broad with a longer inner limb. A large, curved primary cusp with 9–12 irregular denticles is on the masticatory margin on the inside of the cusp. The denticles become decreasingly distinct towards the inner edge of the tooth. On the innermost portion of the masticatory margin is a thickened triangular area. The outer lateral teeth have a single hook-shaped cusp and decrease in size towards the outer limit of the radula.

Central nervous system: The arrangement of ganglia (Figure 29C) is euthyneurous, with a short visceral loop. The cerebral ganglia are large and are separated by a short, but distinct commissure. Additional ganglionic tissue is situated anterodorsally to each cerebral ganglion. The pedal ganglia are situated ventrally to the rest of the nerve ring and are joined to the cerebral ganglia by long connectives and to the pleural ganglia by shorter ones. The pedal ganglia are connected to each other by an even longer connective. The pleural ganglia are separated from the cerebrals by a short connective. The subintestinal and visceral ganglia are immediately posterior to the left pleural ganglion. A curved visceral loop separates the visceral ganglion from the supraintestinal ganglion, which is connected directly to the right pleural ganglion.

Reproductive system: The posterior reproductive system was not mature, with only a small aggregation of reproductive cells. These cells are not clearly differentiated into reproductive organs.

The penis (Figure 29D) is fully developed in the two specimens examined. A short, curved prostate gland empties into an expanded penial sac, which contains several lobes of the penis. A retractor muscle is connected to the penis near the junction of the prostate with the penial sac.

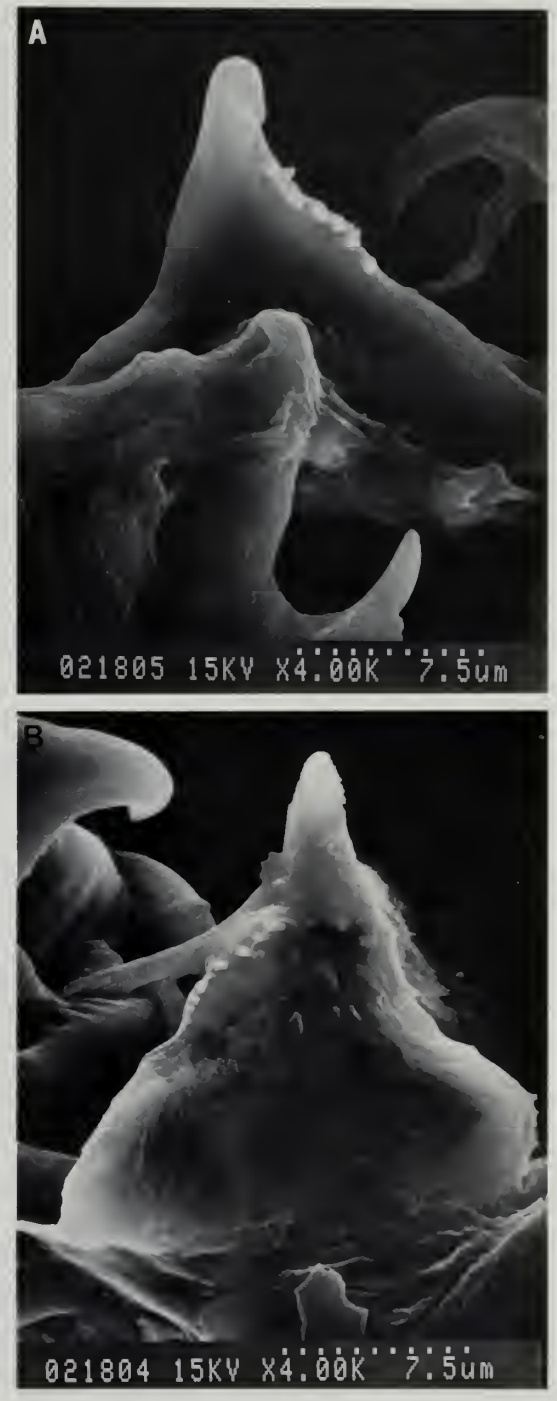

Figure 28

Gastropteron ***hamanni*** Gosliner, sp. nov. A. and B. Scanning electron micrographs of inner lateral teeth.

The primary penial papilla is laterally directed, indented apically, but devoid of any armature. A long duct of the penis sac joins the ciliated sperm groove on the right side of the head.

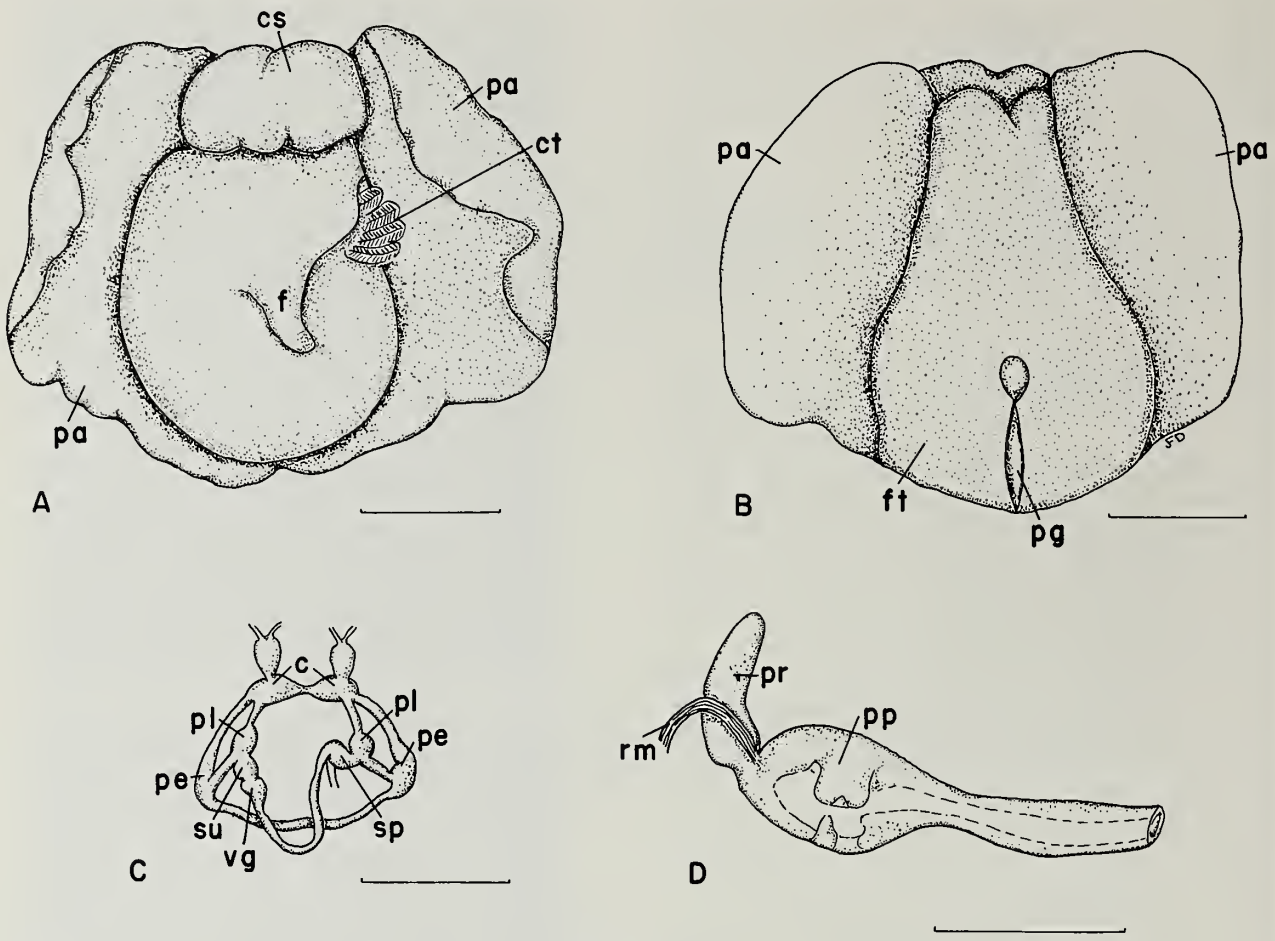

Figure 29

Gastropteron ***odhneri*** Gosliner, sp. nov. A. Dorsal view of preserved animal, scale = 1.0 mm. Key: cs, cephalic shield; ct, ctenidium; f, flagellum; pa, parapodium. B. Ventral view of preserved animal, scale = 1.0 mm. Key: ft, foot; pa, parapodium; pg, pedal gland. C. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglia; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. D. Penis, scale = 0.5 mm. Key: pp, penial papilla; pr, prostate; rm, retractor muscle.

Discussion: *Gastropteron* ***odhneri*** is similar to *G. rubrum* (Rafinesque, 1814), *G. pacificum* Bergh, 1893, *G. sibogae* Bergh, 1905, and *G. japonicum* Tokioka & Baba, 1964, in possessing a large, rounded visceral hump and pinnate, dorsally directed pinnae of the ctenidium. *G.* ***odhneri*** differs from all other members of the genus in having the foot widest posteriorly rather than anteriorly, and in having only 3–5 gill pinnae. All other species have 12–22 leaflets. The jaws of *G.* ***odhneri*** are restricted to a very small portion of the dorsal labial cuticle, whereas in other species they are more widespread. *Gastropteron* ***odhneri*** is the only species in the genus with the denticles on the inner lateral teeth becoming less distinct towards the inner margin. The penial morphology is also unique, with a short curved prostate and a lobed, laterally directed papilla.

Gastropteron sp.

(Figure 31)

Material: One specimen, California Academy of Sciences, San Francisco, CASIZ 066604, Easter Island, Louis de Salvo.

External morphology: The preserved specimen was 2 mm in length. The head shield is roughly triangular with no distinct siphon or siphonal crest. The parapodia are short, not overlapping. The visceral hump is ovoid, and bears a short, simple flagellum on its right side. The gill is small with only a few pinnae.

Shell: A calcified shell is present but, owing to fragmentation, its shape cannot be described.

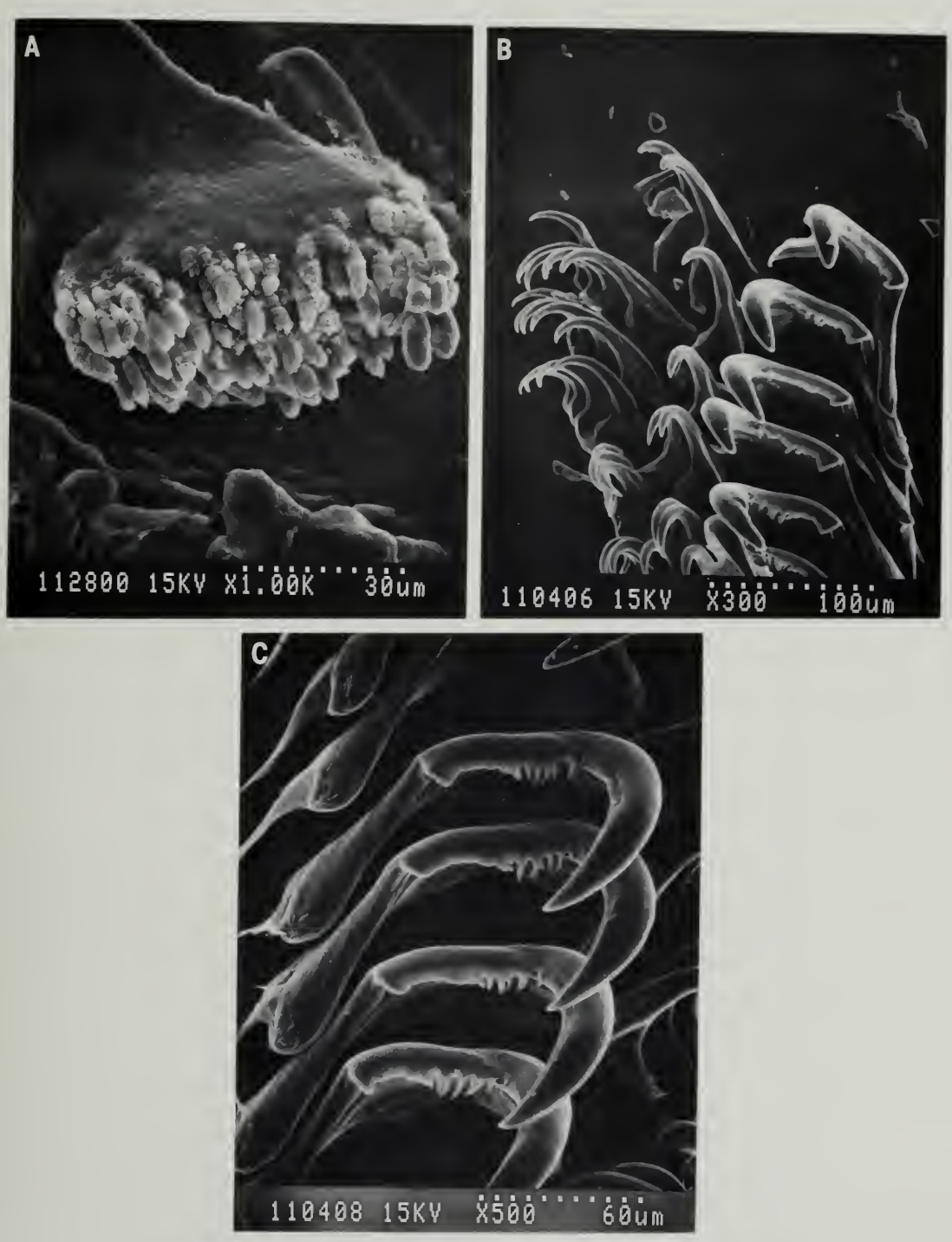

Figure 30

Gastropteron ***odhneri*** Gosliner, sp. nov. Scanning electron micrographs. A. Jaw platelets. B. Half-row of radular teeth. C. Inner lateral teeth.

Digestive system: The buccal mass is short and muscular. The labial cuticle is thin, and apparently devoid of distinct jaw plates. The radular formula is 18 × 2·1·0·1·2. The inner lateral teeth (Figure 31) are broad with an elongate inner limb. A large curved cusp is on the outer edge of the inner lateral. There are 6–9 evenly spaced denticles on the masticatory border. The innermost portion of the masticatory border bears an elongate, triangular cusp. The two

Figure 31

Gastropteron sp., Easter Island. Scanning electron micrograph of half-row of radular teeth.

outer lateral teeth are simple hook-shaped, with the inner one being slightly larger than the outer.

Reproductive system: Details of the posterior reproductive system could not be determined owing to poor preservation. The penis has a short, straight prostate with a simple, conical, unarmed penial papilla.

Discussion: Based on its morphology, with a narrow radula containing only two outer laterals per side, this species appears to be undescribed. However, because only one specimen was collected, without any description of the living animal, it is preferable not to describe it until more material becomes available.

DISCUSSION

Until recently, the Gastropteridae appeared to be a relatively small and morphologically uniform taxon. Members of the family were known largely from temperate waters. Tokioka & Baba (1964), Baba & Tokioka (1965), and Minichev (1967) described several additional taxa from Japan and China, including the distinct genera *Sagaminopteron* and *Enotepteron*. More recently, Carlson & Hoff (1973, 1974) and Hoff & Carlson (1983) described an additional seven species from the tropical western Pacific. Gosliner (1984, 1988a), Gosliner & Armes (1984), and Gosliner & Williams (1988) have added five new species from the southeastern Atlantic, western Atlantic, and western Indian Ocean.

Most of the recently described species inhabit the Indo-Pacific tropics and exhibit considerably more morphological variability than previously believed to occur within the Gastropteridae (Table 2). Table 3 provides the key to each character state for the characters considered.

Character Polarity

In order to discuss the phylogenetic relevance of this variability, it is first necessary to establish the polarity of each character. Members of the Gastropteridae are highly derived cephalaspideans, compared with other members of the Philinacea (Rudman, 1978; Gosliner, 1980, 1981), and possess several autapomorphic features, such as a posterior pedal gland with a longitudinal slit. This fact makes it difficult to determine polarity within the Gastropteridae solely by means of outgroup comparison. For this reason, other criteria such as ontogenetic data or functional arguments are sometimes invoked to supplement outgroup comparison. The numbering system for characters, from 1 to 24, is reiterated in Tables 2 and 3.

1. Shell: Some character polarities can be determined with relative confidence. Loss of the shell in post-metamorphic juveniles and adults is a common apomorphic feature throughout the Opisthobranchia (Gosliner & Ghiselin, 1984; Gosliner, 1988b). The polarity of shell loss is not only supported by outgroup comparison, but by ontogenetic data, where virtually all opisthobranch larvae possess a shell.

2. Siphon: The presence of a siphon at the posterior end of the cephalic shield is an autapomorphy for the family. Presumably the siphon functions as a chemosensory organ analogous to the rhinophores of other opisthobranchs. Because it is absent in other taxa, outgroup comparison provides no information about the polarity of the variation observed in the morphology of the siphon within the Gastropteridae. However, functional arguments, as advocated by Gosliner & Ghiselin (1984), suggest that the elaboration of a medial crest within the siphon provides greater surface area for sensory detection and increases the structural integrity of the siphon. Therefore, the presence of a siphon is considered to represent the apomorphic state.

3. Flagellum: The flagellum, located near the posterior end of the visceral hump, may be homologous to the pallial caecum of other cephalaspideans (*e.g., Acteon* and *Scaphander*). Its position on the right side of the body, posterior to the gill, is similar to that of the pallial caecum. If these structures are indeed homologous, the presence of a flagellum would represent the plesiomorphic state within the Gastropteridae. If the pallial caecum and flagellum are not homologous, the flagellum is autapomorphic within the Gastropteridae. Subsequent cladistic analysis indicates that a flagellum is absent in different lineages of apo-

Table 2

Morphological variation in the Gastropteridae.

Species	Shell	Siphonal crest	Flagellum reduction	Flagellum addition	Gill	Spheres	Tail	Jaws	Outer laterals	Inner lateral	Cerebral commissure	Visceral ganglion	Spermatic bulb	Penial papilla	Penial duct	Penial bulb	Penial spines I	Penial spines II	Swimming	Notched foot	Color	Pigmented border	Pigmented siphon	Convoluted prostrate
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
rubrum	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1
vespertilium	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0
chacmol	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0
hamanni	9	0	1	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	9	0	1	0	1	0
japonicum	0	0	1	0	1	0	0	0	1	1	9	9	9	9	9	9	9	9	9	0	0	0	0	9
bicornutum	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sibogae	0	0	0	0	9	0	0	0	1	5	0	0	9	9	9	9	9	9	9	9	9	9	9	9
pacificum	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
viride	9	0	1	1	1	0	0	2	1	1	9	9	9	9	9	9	9	9	0	0	1	1	0	9
odhneri	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	9	0	9	9	9	0
sp., Easter Island	0	0	0	0	0	0	0	2	1	1	1	9	0	0	0	0	0	0	9	0	9	9	9	0
E. flavum	1	0	0	0	0	2	0	0	1	2	1	1	0	2	0	0	0	0	9	0	0	0	0	0
rosewateri	1	0	0	0	0	1	0	2	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
ornatum	9	1	0	2	2	0	0	2	0	3	9	9	9	9	9	9	9	9	0	1	1	0	1	9
nigropunctatum	0	1	0	0	2	0	0	2	0	3	1	0	0	0	0	0	0	0	0	1	3	0	1	0
bilealbum	0	1	0	0	2	0	0	2	0	3	1	0	0	0	0	0	0	0	0	1	1	0	1	0
psychedelicum	0	1	0	0	2	0	0	0	0	3	1	0	0	0	0	0	0	0	0	1	1	0	1	0
fuscum	1	1	0	0	0	0	0	9	9	9	9	9	9	9	9	9	9	9	9	0	1	1	1	9
pohnpei	1	1	1	0	0	0	0	2	2	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0
ladrones	1	1	0	0	0	0	0	2	2	0	1	1	0	0	1	1	1	0	0	0	1	0	1	0
S. flavum	1	1	1	1	0	0	0	2	2	0	1	0	0	0	1	1	2	0	0	0	2	0	2	0
brunneomarginatum	1	1	0	0	0	0	0	2	2	0	1	0	0	0	1	1	0	0	1	0	2	1	2	0
citrinum	1	1	0	0	0	0	0	2	2	0	1	0	0	0	1	1	0	0	0	0	2	0	2	0
nigromarginatum	1	1	0	0	0	0	0	2	2	0	1	0	0	0	1	1	2	0	0	0	2	1	2	0
michaeli	9	1	1	0	0	0	0	2	2	0	1	0	0	0	1	1	2	0	0	0	2	0	2	0
tigrinum	1	1	0	0	0	0	0	2	2	0	1	0	0	0	1	1	2	0	1	0	2	0	2	0
quadrispinosum	1	1	0	0	0	0	0	0	2	3	1	0	0	0	1	1	1	1	0	0	1	0	1	0
flavobrunneum	0	1	1	0	0	0	0	2	2	4	0	0	1	3	0	0	0	0	0	0	1	0	0	0
alboaurantium	0	1	1	0	0	0	0	2	2	4	0	0	1	0	0	0	0	0	0	0	1	0	1	0
Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24

0 = ancestral; 1–5 = derived states; 9 = missing data.

Table 3

Coding schemes for characters in Table 2.

1. Shell	0 = present	1 = absent	
2. Siphonal crest	0 = absent	1 = present	
3. Flagellum	0 = present	1 = absent	
4. Secondary flagellum	0 = absent	1 = single	2 = multiple
5. Gill	0 = simple	1 = bipinnate	2 = multiple or tripinnate
6. Spheres	0 = absent	1 = sessile	2 = stalked
7. Tail	0 = absent	1 = present	
8. Jaws	0 = well developed	1 = reduced	2 = absent
9. Outer laterals	0 = multiple	1, 2 = reduced number	
10. Inner laterals	0 = simple, denticulate	1 = triangular denticles	2 = few large denticles
	3 = 2 triangular denticles	4, 5 = denticles absent	
11. Cerebral commissure	0 = long	1 = short	
12. Visceral ganglion	0 = distinct	1 = fused	
13. Spermatic bulb	0 = absent	1 = present	
14. Penial papilla	0 = simple	1 = papillate	2 = absent
	3 = apical ring		
15. Penial duct	0 = absent	1 = present	
16. Penial bulb	0 = absent	1 = present	
17. Penial spines I	0 = absent	1 = longitudinal rows	2 = transverse rows
18. Penial spines II	0 = absent	1 = present	
19. Swimming	0 = capable	1 = incapable	
20. Foot	0 = simple	1 = notched	
21. Color	0 = cryptic	1 = aposematic	2 = yellow or orange aposematic
	3 = special resemblance		
22. Pigmented border	0 = absent	1 = present	
23. Pigmented siphon	0 = same color as body	1 = different	2 = brown or black
24. Prostrate	0 = simple	1 = convoluted	

morphic Gastropteridae, further suggesting that its absence represents the derived state.

The flagellum, in most species, is a simple appendage located on the right side of the body. In ***Siphopteron*** *flavum* and *Gastropteron viride* the flagellum is terminal on the posterior end of the visceral hump. These elaborations appear to represent derivations from the ancestral condition. The flagellum is entirely absent in seven species of Gastropteridae (Table 2). This loss has apparently occurred polyphyletically on several occasions within the Gastropteridae.

Burn (1980) speculated that the flagellum has evolved as an accessory copulatory structure, and is related to the presence of penial spines in some members of the family. However, a flagellum is present in many species that lack penial spines. Conversely, at least one species with penial spines, ***Siphopteron*** *michaeli,* entirely lacks a flagellum. *Gastropteron* ***chacmol*** and ***S. quadrispinosum*** have been observed copulating and do not use the flagellum in the process of mating.

4. Additional flagellar appendages: In some species of Gastropteridae the primary flagellum is present, but additional appendages are also present on the posterior portion of the visceral hump. In *Gastropteron bicornutum* a second appendage is present ventral to the primary flagellum. In *Sagaminopteron ornatum* a series of four protuberances is present on the posterior end of the body. These are considered to represent apomorphies within the family.

5. Ctenidium: The ctenidium is simply plicate in virtually all primitive opisthobranchs and is considered here also to represent the plesiomorphic condition in the Gastropteridae. In several more-derived species of *Gastropteron,* the ctenidium has become enlarged and bipinnate. In the case of *Sagaminopteron,* there may be two or more distinct gills. These elaborations, generally present in the larger members of the family, are probably a result of increased respiratory demands.

6. Spheres: In species of *Enotepteron,* the posterior edge of the parapodia bears a pair of spherical appendages. In *E. rosewateri* these are sessile, whereas in *E. flavum* they are stalked. The presence of these structures is considered to be apomorphic within these taxa and stalked appendages appear to be derived from sessile ones, based on their more complex structure. Burn (1980) suggested that these structures have evolved for grasping during copulation. This is unlikely, because neither species has copulatory spines and *E. flavum* entirely lacks a penial papilla (Minichev, 1967). The function of these structures remains unknown.

7. Posterior end of foot: In virtually all cephalaspideans, the posterior end of the foot is short and rounded. This is also the case in most species of Gastropteridae. However, in *Gastropteron bicornutum* the tail possesses an elongate,

filiform extension. This appears to be a derived feature that enhances the resemblance between this species, an undescribed haminoeid, and an undescribed species of *Chelidonura,* all of which are sympatric in Papua New Guinea (Gosliner & Behrens, 1989, in press).

8. Jaws: The presence of a pair of jaws bearing chitinous rodlets is widespread throughout cephalaspidean opisthobranchs and is considered to represent the plesiomorphic state within the subclass (Gosliner, 1980, 1988b). Jaws are reduced in *Gastropteron* ***odhneri*** and absent in many representatives of the Gastropteridae. In the latter cases, only a thin chitinous lining of the buccal mass remains.

9. Outer lateral teeth: Within the cephalaspidean opisthobranchs it is difficult to establish a plesiomorphic radular configuration, owing to extreme variability among primitive members of the clade. However, within the more ancestral Philinacea the plesiomorphic state is well established. Rudman (1978) and Gosliner (1980) have suggested that a larger number of outer lateral teeth per radular row represents the ancestral configuration. This polarity also applies within the Gastropteridae. Species of *Sagaminopteron* have the broadest radulae within the family, and reduction in the number of teeth per row has evolved independently in other members of the family.

10. Inner lateral teeth: Members of the Philinacea are characterized by having a pair of broad inner lateral teeth, each bearing numerous small denticles along its masticatory border (Rudman, 1972, 1978; Gosliner, 1980). This is considered to represent the ancestral condition within the Gastropteridae. In other members of the family, there may be a reduction in the number of denticles. In some cases this appears to involve fusion of denticles to form fewer, larger ones. The most extreme cases involve the loss of all denticles, leaving a smooth masticatory margin. In species of *Gastropteron* there is a triangular thickening on the inner edge of the masticatory border. This structure is not present in any other philinaceans, and is considered to be apomorphic within these Gastropteridae.

11. Cerebral commissure: In virtually all plesimorphic opisthobranchs the cerebral ganglia are well separated from each other by a commissure that is approximately equal in length to the diameter of the cerebral ganglion. This configuration is also present in some species of *Gastropteron* (Gosliner & Armes, 1984), and is considered to represent the plesiomorphic condition for the family. However, in most members of the Gastropteridae the cerebral ganglia are appressed to each other and no distinct commissure is present.

12. Visceral and subintestinal ganglia: In plesimorphic cephalaspidean opisthobranchs, all of the major ganglia are well separated from each other (Gosliner, 1981). The visceral and subintestinal ganglia are distinct in most plesiomorphic opisthobranchs, including most members of the philinacean familes Aglajidae (Rudman, 1974; Gosliner, 1980) and Philinidae (Rudman, 1972; Gosliner, 1988b). On this basis, distinct visceral and subintestinal ganglia are also considered plesiomorphic within the Gastropteridae and their fusion represents the derived condition.

13. Spermatic bulb: With the exception of members of the Acteonacea and one species of *Ringicula,* all cephalaspideans have an open, ciliated sperm groove leading to a cephalic penis. The penis in most cephalaspideans has a simple prostate. In some taxa, such as in many species of *Runcina* (Ghiselin, 1963; Kress, 1977), a spermatic bulb is distinct from the prostate. Ghiselin (1966) considered this to represent an apomorphic state, largely on the basis of functional arguments. In some members of the Gastropteridae (Gosliner, 1984; Gosliner & Armes, 1984) a spermatic bulb is present. However, in these species the bulb enters the penis by means of a separate duct, rather than emptying into the prostate, as in *Runcina.* Nevertheless, this structure is not found in any other cephalaspideans and is considered apomorphic.

14. Penial papilla: In most philinaceans, the penis bears a simple conical papilla, devoid of any elaboration or armature. In the aglajid genus *Melanochlamys,* some species bear a penial stylet or rows of penial spines (Rudman, 1974; Gosliner, in press). These are considered to represent apomorphic states. In *Gastropteron pacificum* Bergh, 1893 (MacFarland, 1966; Gosliner, 1984) there is a row of chitinous processes along the distal margin of the penis. Similarly, in ***Siphopteron*** *flavobrunneum* (Gosliner, 1984) there is a chitinous, subapical penial disc. In *Enotepteron flavum* Minichev, 1967, a penial papilla is entirely wanting. These three states are considered to represent independently evolved apomorphies within the Gastropteridae.

15. Penial duct: In most members of ***Siphopteron,*** a narrow duct connects the anterior end of the prostate to the penial papilla. In the majority of gastropterids and other philinaceans the penial papilla is situated immediately anterior to the prostate, and no separate duct is present. The presence of an additional duct is considered to be apomorphic within the Gastropteridae.

16. Penial bulb: In species of ***Siphopteron*** that have developed a separate penial duct, there is a muscular area immediately anterior to the prostate. This muscular bulb, in turn, joins the penial papilla near the male aperture. This structure is not found in any other philinaceans and is considered apomorphic within the gastropterids.

17. Penial bulb spines: In ***Siphopteron*** *pohnpei, S. citrinum,* and *S. brunneomarginatum,* the penial bulb contains no rows of chitinous hooks. Within the penial bulb of most other members of the genus, are 2–4 rows of chitinous hooks. In some cases, the spines are arranged in longitudinal rows, whereas in other species there is a series of transverse rows. These two conditions are considered to

be independently derived. Both configurations are found in no other philinacean and are considered apomorphic within the Gastropteridae.

18. Large penial spines: In addition to possessing longitudinal rows of chitinous spines within the penial bulb, ***Siphopteron quadrispinosum*** has four large spines situated at the base of the bulb. This is considered a further modification of the penis within the family.

19. Swimming: The overwhelming majority of gastropterids are capable of swimming for long periods of time by flapping their parapodia. This is an autapomorphy for the family. However, several species have never been observed swimming and are unlikely to be capable of doing so. In these species, loss of swimming ability is considered apomorphic, because they are derived in virtually all other aspects of their morphology.

20. Notched foot: In species of *Sagaminopteron,* the anterior end of the foot is medially divided. This occurs in no other cephalaspideans and appears to be apomorphic within the Gastropteridae.

21. Color: Because most opisthobranchs are toxic, cryptic coloration is assumed to have preceded aposematic coloration (Gosliner & Behrens, 1989). Virtually all primitive members of the Philinacea are inconspicuously colored and blend in with their substrate. A few species of *Philine,* which are epifaunal, are brightly colored and appear to exhibit aposematic coloration (Gosliner, 1988a). Many, if not most, species of aglajids are brightly colored and exhibit warning coloration (Gosliner, 1980; Gosliner & Behrens, 1989) Some members of *Gastropteron,* such as *G. pacificum,* blend in well with a generalized substrate. Most members of the genus are brightly colored and probably exhibit aposematic coloration. The same situation occurs in ***Siphopteron,*** where *S. pohnpei* blends in well with its environment and all other members of the genus are brilliantly colored. ***Siphopteron*** *citrinum, S. brunneomarginatum, S. michaeli, S. flavum,* ***S. tigrinum,*** and ***S. nigromarginatum*** all are yellowish or orange with brown or black pigment. This color pattern appears to be a derived feature uniting these taxa.

Species of *Sagaminopteron* are either brightly colored or bear special resemblance to their sponge prey. In this case, both are considered to represent derivations from a more generalized, cryptic color pattern.

22. Pigmented parapodial margin: In several members of the Gastropteridae, the margins of the parapodia strikingly contrast with the remainder of the body color. This is considered to represent a derived feature, which has arisen independently within different lineages of gastropterids.

23. Pigmented siphon: In species of gastropterids, the siphon, like the parapodial margin, may be of a contrasting color with respect to the rest of the body. Because the coloration of the siphon is poorly correlated with the development of pigment on the parapodial margin, they are treated as distinct characters.

24. Prostate gland: Within the Philinacea, virtually all species possess a simple, short prostate gland at the posterior end of the cephalic penis. In some taxa, such as *Gastropteron rubrum* and *G. pacificum,* the prostate is elongate and highly convoluted. This is a modification of the plesiomorphic condition.

Phylogeny of the Gastropteridae

Having hypothesized the polarity of these characters, many phylogenetic analyses were performed using Phylogenetic Analysis Using Parsimony (PAUP). The data to construct phylogenetic analysis are provided in Tables 2 and 3. Many of the examined characters have multiple derived character states. In virtually every case, these are considered as unordered characters. This assumes that the sequence of change of the various derived states from the ancestral condition is unknown. However, in the case of the parapodial spheres, stalked spheres are assumed to be derived from sessile ones. Similarly, reduced jaw plates are assumed to be intermediate between ancestrally well-developed jaws and more-derived jaws that entirely lack plates.

These analyses produced an array of different most-parsimonious trees, depending on the combination of characters and taxa included, and the ordering of characters. The likelihood of these trees reflecting the true phylogeny of the Gastropteridae was then ascertained. A tree may be parsimonious in that it requires a minimum number of character transformation steps, but is not parsimonious from a functional point of view. For example, one family of trees required the evolution of a spermatic bulb from the hypothetical ancestor to *Gastropteron vespertilium,* its loss in other species of *Gastropteron,* its subsequent re-evolution in two species of ***Siphopteron*** and, finally, its loss again in other members of the genus. Complex characters such as the spermatic bulb are unlikely to undergo such multiple gains and reversals. A more parsimonious scenario for that character involves the development of a spermatic bulb in two independent lineages, once within *G. vespertilium* and again in *S. alboaurantium* and *S. flavobrunneum.* Other trees required the reduction of numbers of outer lateral teeth, their subsequent increase, followed by another decrease. Once radular teeth are lost in opisthobranchs, there is no evidence that they can be increased again in more apomorphic lineages. These scenarios also require the evolution of penial bulb spines, their loss, and re-evolution. These suggested character transformations may require fewer evolutionary steps, but are not parsimonious with what we know about character evolution within opisthobranchs.

Based upon phylogenetic analysis using PAUP and subsequent scrutiny of the required transformations, the fol-

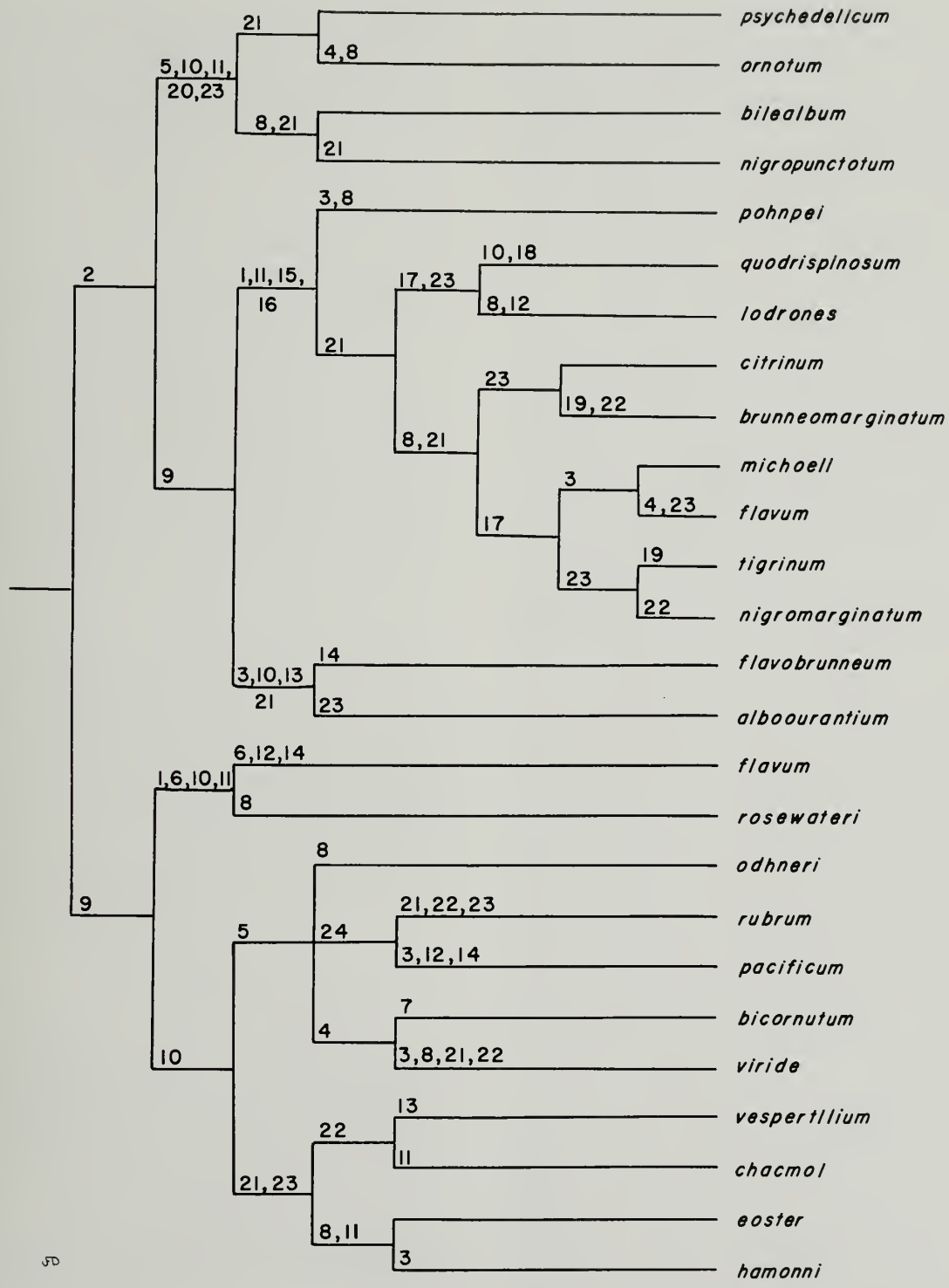

Figure 32

Phylogenetic relationships of the Gastropteridae.

lowing phylogenetic tree was produced (Figure 32). It requires 76 steps, three more than the most parsimonious tree produced using the same characters and taxa with PAUP. However, it is considered preferable because it reduces reversal and emphasizes the monophyly of some structures such as the prominent siphonal crest and complex penial structures. Other characters, such as reduction of the number of rows of radular teeth and the loss of the flagellum, are far more likely to occur many times within and between lineages.

Generic Divisions within the Gastropteridae

Previously, three genera of Gastropteridae have been described, *Gastropteron* Meckel *in* Kosse, 1813, *Sagaminopteron* Tokioka & Baba, 1964, and *Enotepteron* Minichev, 1967. *Sagaminopteron* was erected to accommodate *S. ornatum,* with two prominent denticles on the inner lateral teeth and a large number of outer lateral teeth. The addition of *S. nigropunctatum* Carlson & Hoff, 1973, *S. bilealbum* Carlson & Hoff, 1973, and *S. psychedelicum* Carlson & Hoff, 1974, confirms these attributes for the genus, though a large number of outer laterals appears to be plesiomorphic. Members of the genus have additional synapomorphies. Together with species of ***Siphopteron,*** members of *Sagaminopteron* have a prominent medial siphonal crest. Species of *Sagaminopteron* also have an elaborated gill with distinct pinnations on each pinna, appressed cerebral ganglia, and a notched anterior border of the foot. Plesiomorphic features include a well-calcified shell, a flagellum on the right side of the body, distinct subintestinal and visceral ganglia, and a simple penis.

Enotepteron was described to include the monotypic species *E. flavum* Minichev, 1967. It was distinguished by having a pair of stalked spheres on the posterior end of the parapodia, inner lateral teeth with a few, large denticles, and a lack of a penial papilla. With the addition of *E. rosewateri* Gosliner, 1988, the presence of spheres on the parapodia and large denticles on the inner lateral teeth characterize the genus. Other apomorphies include an absence of a shell and appressed cerebral ganglia. Plesiomorphic features include a siphon without a medial crest, simple flagellum and gill, and a simple penis, with or without a papilla.

All other species were included in *Gastropteron* (Tokioka & Baba, 1964; Baba & Tokioka, 1965; Carlson & Hoff, 1974; Hoff & Carlson, 1983; Gosliner, 1984; Gosliner & Armes, 1984; Gosliner, 1988a; Gosliner & Williams, 1988), largely because they have fewer lateral teeth than in *Sagaminopteron.* What has become apparent is that there is considerably more morphological variability in these taxa than previously known. From the cladogram (Figure 32), it is apparent that several of these taxa form a monophyletic unit, distinct from *Gastropteron.* In each of the approximately 50 phylogenetic analyses that were conducted using PAUP, these taxa always formed a natural group. They are united by several apomorphic features, including a reduced number of outer lateral teeth and a modified penis that contains either a spermatic bulb or penial bulb, with or without spines. Together with members of *Sagaminopteron,* they have a prominent medial crest on the siphon. On the basis of these apomorphies, these taxa can be clearly distinguished from species of *Gastropteron,* and are, therefore, placed in the new genus ***Siphopteron.*** The fact that members of this genus and *Sagaminopteron* have a prominent siphonal crest suggests that these two genera are more closely allied to each other than to *Gastropteron* and *Enotepteron.*

Once species of ***Siphopteron*** are removed from *Gastropteron,* it is necessary to determine what apomorphic features unite the remaining members of the genus. One feature stands out. All species have a prominent triangular extension on the inner margin of the inner lateral teeth. Plesiomorphic features include a shell, lack of a siphonal crest (together with species of *Enotepteron*), lack of a penial duct or penial bulb, and a truncate anterior end of the foot.

Based on this division of the family, the constituent members of the family are included in the following genera. Type species are indicated by an asterisk (*):

Gastropteron Meckel *in* Kosse, 1813

**Gastropteron rubrum* (Rafinesque, 1814)
Gastropteron bicornutum Baba & Tokioka, 1965
Gastropteron ***chacmol*** Gosliner, sp. nov.
Gastropteron ***hamanni*** Gosliner, sp. nov.
Gastropteron japonicum Tokioka & Baba, 1964
Gastropteron ***odhneri*** Gosliner, sp. nov.
Gastropteron pacificum Bergh, 1893
Gastropteron sibogae Bergh, 1905
Gastropteron vespertilium Gosliner & Armes, 1984
Gastropteron viride Tokioka & Baba, 1964

Enotepteron Minichev, 1967

**Enotepteron flavum* Minichev, 1967
Enotepteron rosewateri Gosliner, 1988

Sagaminopteron Tokioka & Baba, 1964

**Sagaminopteron ornatum* Tokioka & Baba, 1964
Sagaminopteron bilealbum Carlson & Hoff, 1973
Sagaminopteron nigropunctatum Carlson & Hoff, 1973
Sagaminopteron psychedelicum Carlson & Hoff, 1974

Siphopteron gen. nov.

****Siphopteron tigrinum*** Gosliner, sp. nov.
Siphopteron *alboaurantium* (Gosliner, 1984) comb. nov.
Siphopteron *brunneomarginatum* (Carlson & Hoff, 1974) comb. nov.
Siphopteron *citrinum* (Carlson & Hoff, 1974) comb. nov.
Siphopteron *flavobrunneum* (Gosliner, 1984) comb. nov.
Siphopteron *flavum* (Tokioka & Baba, 1964) comb. nov.
Siphopteron *fuscum* (Baba & Tokioka, 1965) comb. nov.
Siphopteron *ladrones* (Carlson & Hoff, 1974) comb. nov.

Siphopteron *michaeli* (Gosliner & Williams, 1988) comb. nov.
Siphopteron nigromarginatum Gosliner, sp. nov.
Siphopteron *pohnpei* (Hoff & Carlson, 1983) comb. nov.
Siphopteron quadrispinosum Gosliner, sp. nov.

Incertae sedis

Gastropteron sinense A. Adams, 1861.

Taxonomy of Species of Gastropteridae

The above arrangement of species within gastropterid genera is somewhat tentative, owing to the incomplete description of several taxa. *Gastropteron japonicum* Tokioka & Baba, 1964, is clearly placed within *Gastropteron*, based on its external and radular morphology. However, Tokioka & Baba (1964) noted its similarity to *G. pacificum*, and stated that it differs in having fewer (13) gill pinnae than *G. pacificum* (16–20). Because the penial morphology of the former remains undescribed, the separation of the two species remains tentative. *Gastropteron sibogae* Bergh, 1905, is incompletely described and its penial morphology remains unknown. However, it appears to be distinct from other members of the genus, as it lacks denticles on the inner lateral teeth. *Gastropteron viride* Tokioka & Baba, 1964, has a gill similar in shape to that of *G. rubrum*, *G. pacificum*, *G. japonicum*, *G. bicornutum*, and *G.* ***odhneri***, but differs from all of these in having modified inner and outer lateral teeth and in having a terminal knob on the posterior of the visceral hump, as in ***Siphopteron*** *flavum*. The penial morphology of *G. viride* remains unknown.

The internal morphology of ***Siphopteron*** *fuscum* Baba & Tokioka, 1965, remains unknown. However, its distinctive color pattern ensures that it is separable from all known members of the family. It is placed within ***Siphopteron*** because of its small body size, prominent siphonal crest, and reduced ctenidium.

Biogeography of the Gastropteridae

Within the family Gastropteridae, the genus *Gastropteron* is the most widespread with both temperate and tropical taxa in all the world's oceans. *Gastropteron rubrum* is known from the Mediterranean and West Africa (not from the western Atlantic, see discussion of *G.* ***chacmol***). Two species, *G. vespertilium* and *G.* ***chacmol***, are known from the western Atlantic. *Gastropteron pacificum* is known from Alaska to the Gulf of California and possibly Japan, if it is conspecific with *G. japonicum*. The tropical Indo-Pacific species *G. bicornutum* is known from Japan and Papua New Guinea. The remaining species are known only from their type localities.

Members of *Enotepteron* and *Sagaminopteron* are known from the Indo-Pacific tropics, with the exception of *E. flavum*, which is subtropical in the Indo-Pacific. *Sagaminopteron ornatum* is known from Japan and Australia (Richard Willan, pers. comm.) and *S. psychedelicum* is known from the Marianas Islands, Papua New Guinea, and Reunion Island. The remaining species are known only from the type localities.

Virtually all species of ***Siphopteron*** are known only from the Indo-Pacific tropics, the exceptions being *S. alboaurantium* and *S. flavobrunneum*, which are known only from the Atlantic coast of the Cape of Good Hope Peninsula, South Africa. It should be noted that many endemic southern African species have historical biogeographical links with the Indo-Pacific tropics (Gosliner, 1987). The phylogenetic analysis provided here would also suggest that this is indeed the case for these taxa. Several members of this genus are widespread. For example, *S. ladrones* is known from Aldabra, in the western Indian Ocean and Guam, and *S.* ***tigrinum*** is known from Palau, New Guinea, Australia, and Madagascar. Several other species are widespread in the Pacific Ocean, but have not been found in the Indian Ocean. ***Siphopteron quadrispinosum*** is known from Papua New Guinea and Hawaii and *S. pohnpei* is known from Ponape and Hawaii. ***Siphopteron*** *flavum* and *S. brunneomarginatum* are widespread in the western Pacific Ocean. The remaining species are known only from their original description.

Most of the evolution within the Gastropteridae has apparently occurred within the Indo-Pacific tropics.

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A New Species of the Genus *Thordisa* (Mollusca: Nudibranchia) from the Southwestern Iberian Peninsula

by

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Abstract. A new species of nudibranch mollusk, *Thordisa* ***azmanii,*** is described from the southwestern Iberian Peninsula, Spain. Its coloration and anatomy distinguish it from the remaining Mediterranean and Atlantic species of *Thordisa.*

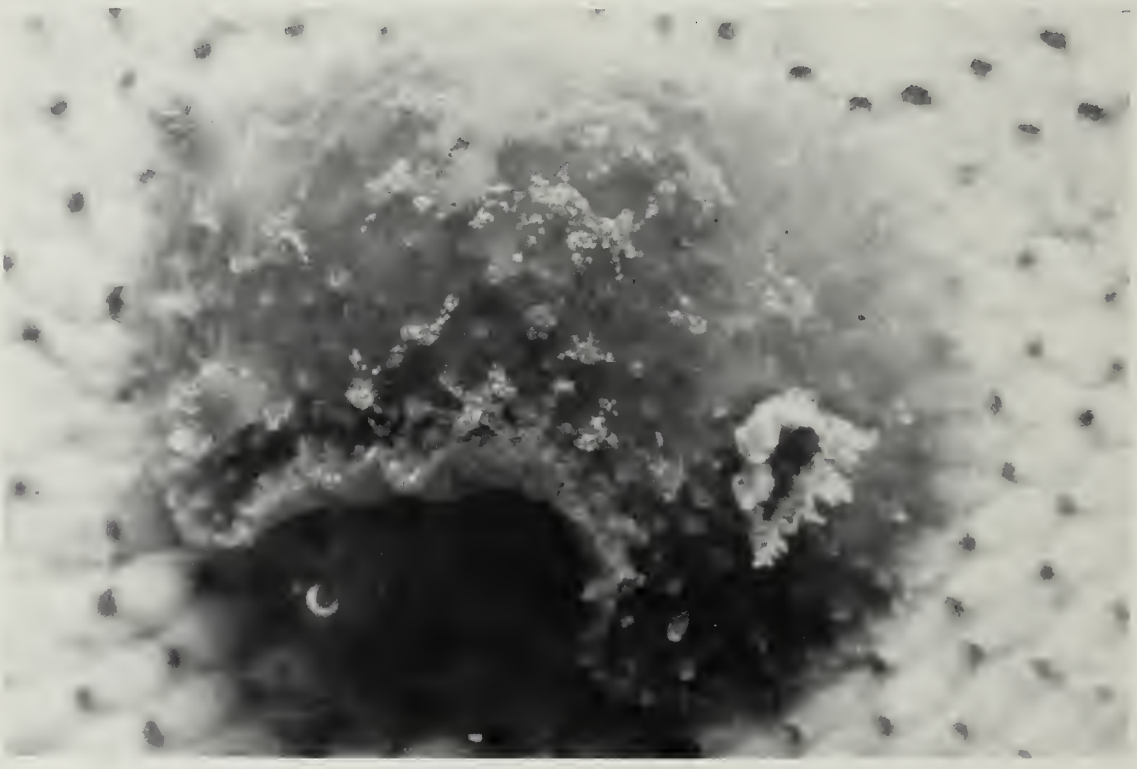

Figure 1

Thordisa ***azmanii*** sp. nov. Living animal, 11-mm specimen collected from Santa María del Mar Beach (Cádiz, Spain).

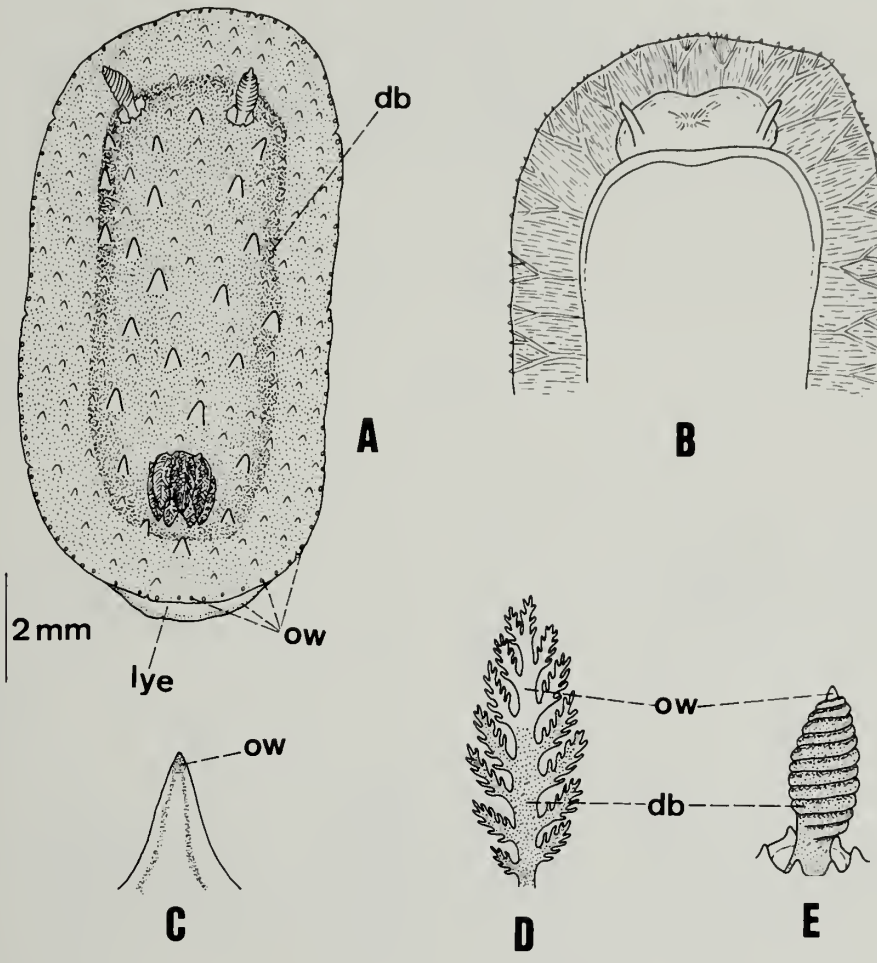

Figure 2

Thordisa ***azmanii***. A. Dorsal view. B. Ventral view of anterior end. C. Detail of mantle tubercle. D. Gill. E. Rhinophore. Key: db, dark brown; lye, light yellow; ow, opaque white.

INTRODUCTION

Three specimens of a new doridacean have been collected at the southwestern Iberian Peninsula, Spain. Their external and internal anatomical features agree with species of the genus *Thordisa* Bergh, 1877 (type *T. maculigera* Bergh, 1877), although they differ from known Mediterranean and European species: *T. pallida* Bergh, 1884, *T. aurea* Pruvot-Fol, 1951, and *T. filix* Pruvot-Fol, 1951. This latter species has recently been recorded by BALLESTEROS (1987) and TEMPLADO *et al.* (1988) from the Iberian coasts.

Thordisa ***azmanii*** Cervera & García-Gómez, sp. nov.

(Figures 1–4)

Material examined: (1) Holotype: One specimen, 11 mm in length, collected intertidally under stones at Santa María del Mar Beach (Cádiz, Spain), 36°31'N, 6°17'W, April 1985, deposited in the Museo Nacional de Ciencias Naturales de Madrid (Spain), catalogue number 12-77/1028.

(2) Paratypes: One specimen, 13 mm in length, collected intertidally under stones at Santa María del Mar Beach (Cádiz, Spain), June 1985, deposited in the Laboratorio de Biología Marina, Departamento de Fisiología y Biología Animal, Universidad de Sevilla.

(3) One specimen, 5 mm in length, collected intertidally under stones at Santa María del Mar Beach (Cádiz, Spain), January 1986, deposited in the Laboratorio de Biología Marina, Departamento de Fisiología y Biología Animal, Universidad de Sevilla. Color transparencies of living *Thordisa* ***azmanii*** are on file at the Laboratorio de Biología Marina, Departamento de Fisiología y Biología Animal, Universidad de Sevilla.

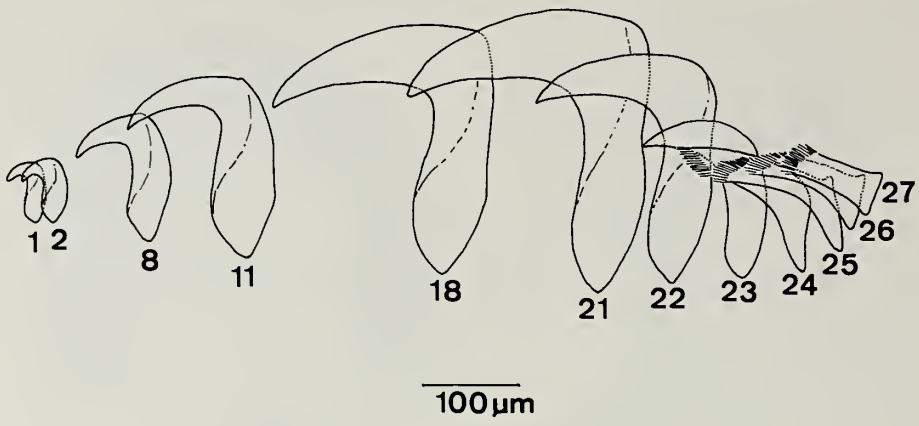

Figure 3

Thordisa ***azmanii***. Half-row of radular teeth.

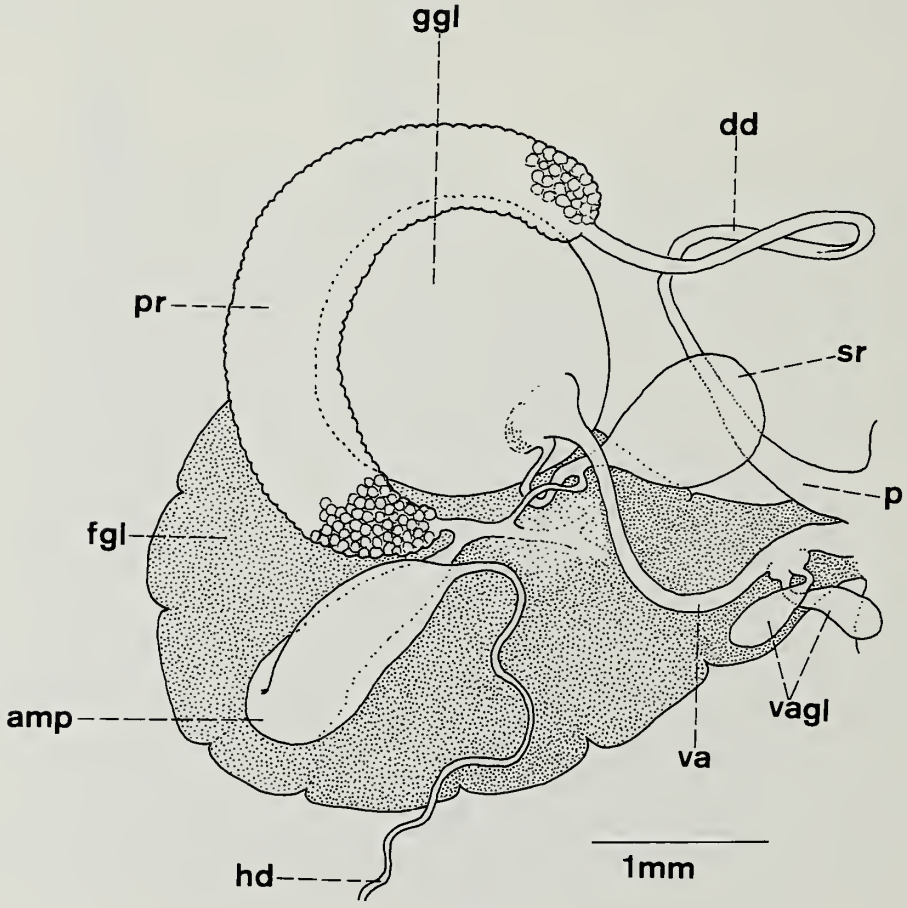

Figure 4

Thordisa ***azmanii***. Reproductive system. Key: amp, ampulla; dd, deferent duct; fgl, female gland; ggl, gametolytic gland; hd, hermaphroditic duct; p, penis; pr, prostate; sr, seminal receptacle; vagl, vaginal glands; vd, vaginal duct.

Table 1

Comparison between the Mediterranean and Atlantic species of *Thordisa*.

Species	Mantle tubercles	Ground color	Foot color	Gills	Smooth labial cuticle	Radula	Unarmed penis	Vaginal glands	References
T. pallida Bergh, 1884	little different nodules	yellowish white	?	10 tripinnate gills; color similar to ground color	+	hooked, smooth teeth; marginals slightly denticled	+	1, more or less spherical (quoted as vestibular gland)	BERGH (1884); PRUVOT-FOL (1954)
T. filix Pruvot-Fol, 1951	slender, long and different; grayish-red color	dark yellowish or orange, with delicate brown dots	light yellow or orange	4 bipinnate gray gills, with white rachis	+	hooked, smooth teeth; marginals slender, pectinate on edges	+	1, tubular, highly elongate and coiled on itself	PRUVOT-FOL (1951, 1954); SCHMEKEL (1970); SCHMEKEL & PORTMANN (1982)
T. aurea Pruvot-Fol, 1951	small and short	yellow lemon	?	6–8 bipinnate gills; color similar to ground color	?	similar to *T. filix*	?	?	PRUVOT-FOL (1951, 1954)
T. diuda Marcus, 1955	conical and rough, different in form and size; paler than the ground color, with white pigmentation	olivaceous; brown	orange anterior and white posterior; cream	6 tri- or bipinnate gills; base dark brown, clearer up to apex	+	hooked, smooth teeth; pectinate marginals	+	1, with lobes	MARCUS (1955); THOMPSON (1980)
*T. ladislavii** (Ihering, 1886)	hemispherical and smooth	brown	light brown	4 or 5 tripinnate gills; color similar to mantle	+	hooked, smooth teeth; pectinate and degenerate marginals	+	?	IHERING (1886)
T. punctulifera† Bergh, 1907	small and almost conical; white	white with black spots	white, sometimes with black spots on the edge	5 white tripinnate gills	+	hooked, smooth teeth; pectinate marginals	+	?	BERGH (1907)
T. azmanii sp. nov.	conical and different in size; larger with opaque white pigmentation	dark brown	light yellow, with delicate opaque white on posterior edge	5–7 bipinnate gills; opaque white apex, rest of gill dark brown	+‡	hooked, smooth teeth; pectinate marginals	+	2, elongate	present study

* Live specimens not seen.

† The specimens from New Caledonia that RISBEC (1953) attributes to *T. punctulifera* and includes in *Carminodoris* do not correspond to this species because the radula described by this author is different from that described by BERGH (1907) for *T. punctulifera*. Moreover, *Carminodoris* has an armed penis.

‡ Lacks discrete armature.

Description: The body is oval, somewhat convex and spiculose (Figure 1). The mantle is covered by conical tubercles varying in size, although the small ones are generally arranged at the mantle, rhinophoral sheath, and branchial sheath edges (Figures 1, 2A). Spicules are located within the tubercles. Ventrally, radial and branched bundles of spicules are visible in the mantle (Figure 2B). The bilabiate foot, spiculose, is not notched and occasionally extends posteriorly from the mantle edge. The oral tentacles are short and cylindrical. The rhinophores possess 9–11 lamellae (Figure 2E). The branchial tuft has 5–7 bipinnate gills (Figure 2D), which surround the anal papilla.

The ground color of the mantle is dark brown, and its edges bear small opaque white spots. The larger tubercles usually exhibit an irregular opaque white pigmentation throughout their length. The rhinophores are dark brown with opaque white tips on the 3 or 4 apical rhinophoral lamellae. A little more than the proximal half of each gill is dark brown and the remaining part is opaque white (Figures 1, 2A, C–E). The light yellow foot, possesses a minutely opaque white pigmentation on its posterior edge (Figure 2A).

The labial cuticle lacks discrete armature. The radular formula of one 13-mm specimen is 31 × 4·23·0·23·4. The teeth (Figure 3) are hooked and smooth, except the four marginals, which are pectinate. The inner teeth are small with respect to those in the middle of each half-row. From the 21st tooth, the size of the teeth rapidly decreases.

The thin hermaphroditic duct of the reproductive system (Figure 4) connects with a large ampulla that folds upon itself. The granular prostate partially covers the gametolytic gland and joins the unarmed penis by a long and slightly coiled deferent duct. The spherical gametolytic gland is voluminous and the pyriform seminal receptacle is smaller. The vaginal duct is relatively long. Two elongate vaginal glands connect with this duct close to its external opening.

Discussion: The main external and internal features of *Thordisa* ***azmanii*** are compared with those of known Mediterranean and Atlantic species of the genus *Thordisa* in Table 1.

Thordisa ***azmanii*** is the only species of *Thordisa* recorded from northeastern Atlantic coasts and it can be distinguished well from the Mediterranean species (*T. pallida* Bergh, 1884; *T. aurea* Pruvot-Fol, 1951; and *T. filix* Pruvot-Fol, 1951) by its coloration, the shape of the mantle tubercles and marginal teeth, and the possession of two vaginal glands. The former and latter features also distinguish *T.* ***azmanii*** from other Atlantic species of the genus.

The British species *Doris millegrana* Alder & Hancock, 1854, recently placed in *Discodoris* by Thompson & Brown (1981, 1984), has a similar radula to *Thordisa* species, but the 4–6 outer lateral teeth of *Doris millegrana* are denticled. Some authors suggested previously the possibility that this species belongs to the genus *Thordisa* (Bergh, 1891, 1894; Eliot, 1910; Odhner *in* Marcus, 1955; Marcus & Marcus, 1967), but examination of more material is required to change the generic placement of this species.

The specific name ***azmanii*** is chosen to give recognition to Dr. J. Azmani (M.D.), who eliminated a chronic ailment of one of us (J. C. García-Gómez).

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Studies on the Feeding Behavior and Host Specificity of a Tropical Ectoparasitic Snail in the Genus *Odostomia* (Pyramidellidae)

by

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Abstract. Snails in the genus *Odostomia* Fleming, 1813, are common intertidal ectoparasites in Panama Bay, Republic of Panama, yet nothing is known about their feeding behavior or host specificity. Evidence is presented indicating that one species, *Odostomia* (*Chrysallida*) *communis* (C. B. Adams, 1852), predominantly parasitizes serpulid polychaete worms (Serpulidae). Like many North American and European pyramidellids, however, *O. communis* is not host specific and will also feed on several sympatric species of bivalves. A distinct searching behavior that may aid in locating hosts at a distance is described for these snails.

INTRODUCTION

Snails in the family Pyramidellidae are marine ectoparasites that feed on the body fluids of many invertebrates including polychaetes, gastropods, and bivalves (*e.g.*, FRETTER & GRAHAM, 1949a, b; ROBERTSON, 1957; ALLEN, 1958; ANKEL, 1959; SCHELTEMA, 1965; WELLS & WELLS, 1969; ROBERTSON & MAU-LASTOVICKA, 1979) and, in some cases, polyplacophorans and echinoderms (for a review see ROBERTSON & ORR, 1961). These ectoparasites have an eversible proboscis that can be attached to their hosts using an oral sucker located at the distal end. Once attached, the snail perforates the host's body wall with a pinlike stylet, and sucks blood and perhaps tissue debris by means of a buccal pump (FRETTER & GRAHAM, 1949b).

Early studies suggested that members of this family were host specific, parasitizing individuals of only one species (FRETTER & GRAHAM, 1949a, b, 1962). It is now recognized, however, that many pyramidellids are generalists, capable of feeding on a variety of hosts to some extent (ALLEN, 1958; ANKEL & CHRISTENSEN, 1963; BOSS & MERRILL, 1965; SCHELTEMA, 1965; BULLOCK & BOSS, 1971; ROBERTSON & MAU-LASTOVICKA, 1979). Although many pyramidellids are not strictly host specific, most have a preferred host, one that is parasitized the majority of the time (BOSS & MERRILL, 1965; ROBERTSON & MAU-LASTOVICKA, 1979). Primary and secondary hosts for many North American and European pyramidellids have been reported, along with the feeding and host-selection behavior of these ectoparasites (*e.g.*, COLE, 1951; COLE & HANCOCK, 1955; LOOSANOFF, 1956; ALLEN, 1958; ANKEL, 1959; ROBERTSON & ORR, 1961; ANKEL & CHRISTENSEN, 1963; SCHELTEMA, 1965; BOSS & MERRILL, 1965; WELLS & WELLS, 1969; ROBERTSON & MAU-LASTOVICKA, 1979).

Although much literature pertains to North American and European pyramidellids, almost nothing is known about the feeding behavior and host specificity of tropical pyramidellids, especially in tropical west America. In the genus *Odostomia* Fleming, 1813, alone, about 100 species are described from the Panamic province. The degree of host preference and specificity for these tropical snails has yet to be worked out (KEEN, 1971). The need for research on west American pyramidellids is particularly important because the greatest concentration of pyramidellids appears to be in the Pacific Ocean (LASERON, 1959).

Many pyramidellids are highly motile, frequently moving on and off hosts, spending time on the substratum (ANKEL & CHRISTENSEN, 1963; SCHELTEMA, 1965; BOSS & MERRILL, 1965; WHITE *et al.*, 1984) and perhaps on non-host organisms (ROBERTSON & ORR, 1961; ROBERTSON & MAU-LASTOVICKA, 1979). Therefore, the mere presence of a pyramidellid on or with another invertebrate is not proof that the invertebrate in question is host to the pyramidellid (ROBERTSON & ORR, 1961). ROBERTSON & MAU-LASTOVICKA (1979) suggested that to establish a host-ectoparasite relationship between an invertebrate and a pyramidellid, investigators need to demonstrate a consistent association with organisms in the field and then to

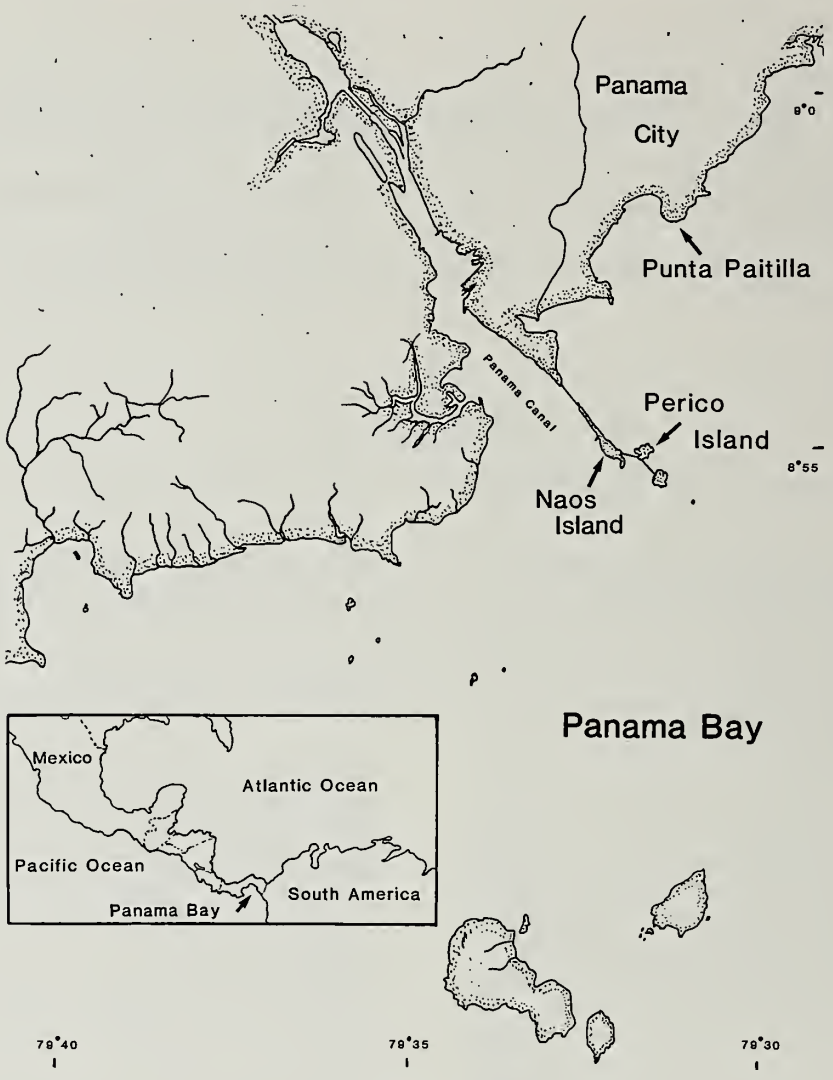

Figure 1

Study area in Panama Bay, Republic of Panama. Collections were made at Punta Paitilla and Perico Island.

determine whether these potential hosts are fed on in the laboratory. In this study, feeding behavior and host specificity of a tropical pyramidellid in the genus *Odostomia* were determined. Using field and laboratory observations and laboratory choice experiments I addressed the following questions: (1) Are these snails consistently associated with certain invertebrates in the field? (2) Which organisms will they feed on in the laboratory? (3) Which organisms are these snails attracted to in the laboratory? This research was conducted between September and December 1984, at the Smithsonian Tropical Research Institute, Naos Island laboratory, Panama City, Republic of Panama (08°55′N, 79°32′W).

MATERIALS AND METHODS

Field Investigations

Field observations and collecting were conducted at two similar sites in the rocky intertidal zone at Punta Paitilla and Perico Island in Panama Bay (Figure 1). Specimens of pyramidellids found within and around tidal pools were collected, and the two most abundant species sent to Mr. Miguel C. Aviles E. at the Department of Zoology, University of Panama, Republic of Panama. Mr. Aviles identified the larger snail as *Odostomia* (*Chrysallida*) *communis* (C. B. Adams, 1852) (Figure 2A) and the smaller snail as *Odostomia inconspicua* (C. B. Adams, 1852) (Figure 2B).

Figure 2

Scanning electron micrographs of ectoparasitic pyramidellids collected at Punta Paitilla and Perico Island, Panama Bay, Republic of Panama. Bars equal 1.0 mm. A. *Odostomia communis* (C. B. Adams, 1852). B. *Odostomia inconspicua* (C. B. Adams, 1852).

Representative samples of these snails are on deposit at the Academy of Natural Sciences of Philadelphia, Pennsylvania (ANSP A12637 and A10624A, respectively). Shell characteristics of these two species were also compared with the descriptions given by DALL & BARTSCH (1909), and were found to be consistent with those of *O. communis* and *O. inconspicua*. In addition, I collected several small (<1.0 mm) unidentified pyramidellids, and several individuals I identified as *Odostomia* (*Chrysallida*) *tyleri* Dall & Bartsch, 1909. All identifications were based on conchological characteristics, and therefore supraspecific designations should be considered tentative (ROBERTSON, 1978).

To determine with which organisms *Odostomia* spp. were associated, I haphazardly collected a total of 48 rocks and shells of approximately the same size (10–20 cm) from tide pools at both sites. For each rock or shell (henceforth designated as sampled substrata) an estimate was made of the percentage of area in each of three categories: (1) area covered by serpulid polychaetes (all species), (2) area covered by other encrusting macroorganisms including sponges, bryozoans, non-motile gastropods, and bivalves, and (3) area not covered by any macroorganism. In addition, the number of *Odostomia* spp. associated with organisms in each of these categories was recorded. The criterion for association was established as the location of a snail within one shell height from a suspected host. This distance was easily within reach of the ectoparasite's proboscis, which

can be extended at least two times the shell height. In the field, it was difficult to distinguish species of *Odostomia,* owing to their small size (1–4 mm). Consequently, data are reported as the number of associated *Odostomia* spp., and represent snails in several species.

Data for the percentage of area covered by each of the three categories was scored from 0 to 10, with 10 being approximately 100% of the sampled substrata covered by a given category. A non-parametric Kruskal-Wallis test, followed by a non-parametric SNK procedure, was used to test for differences in the area covered by, and in numbers of *Odostomia* spp. associated with, each of the three categories. A non-parametric test was used because data were severely heteroscedastic and non-normal.

Indices of dispersion (I) were calculated for snails associated with each of the three categories using an s^2 to $\bar{x}$ ratio. Pieces of sampled substrata were used as the sampling units ($n = 48$). The normal variable d was then calculated from I and compared to critical values (ELLIOTT, 1977).

Feeding Observations

Ectoparasites and organisms with which they were associated in the field were taken to the laboratory for further observations. Ten to 15 individuals of *Odostomia communis* were placed in a large finger-bowl filled with seawater (26–30°C) and offered suspected host organisms two or three species at a time, including: (1) serpulid polychaetes (several unidentified species), (2) *Isognomon recognitus* (Mabille, 1895) (Bivalvia), (3) *Arcopsis solida* (Sowerby, 1833) (Bivalvia), (4) *Chama echinata* Broderip, 1835 (Bivalvia), (5) *Ostrea palmula* Carpenter, 1857 (Bivalvia), (6) *Lithophaga aristata* (Dillwyn, 1817) (Bivalvia), (7) *Tellina* sp. (Bivalvia), (8) columbellid gastropod (Columbellidae), (9) vermetid gastropod (Vermetidae), (10) tunicates, (11) encrusting sponges, and (12) colonial bryozoans. Observations on the feeding behavior of *Odostomia communis* were made using a dissecting microscope over 8-h periods on nine different days.

Choice Experiments

Based on feeding observations of *Odostomia communis,* I selected five test organisms for choice experiments: (1) serpulid polychaetes, (2) *Isognomon recognitus,* (3) *Arcopsis solida,* (4) *Chama echinata,* and (5) *Ostrea palmula.* Test organisms were scrubbed to remove fouling material and weighed. Approximately equal weights of test organisms were used in each experiment; therefore, several individuals of the smaller species were used in order to obtain comparable live weights. All serpulids used in the experiments were encrusted onto small rocks and live weights were difficult to obtain. Consequently, 15–20 living serpulids of about the same size were used.

For each experiment, individuals of the five test organisms were placed in a large fingerbowl equidistant from the center and close to the sides of the bowl. The fingerbowl was filled with seawater (26–30°C), and an airstone was suspended in the center of the bowl to provide mixing. Twenty-six to 30 starved (24 h) *Odostomia communis* were then placed in the center of the bowl below the airstone and allowed to move freely for 3 h. At the end of the experiment all test organisms were examined, and the number of snails associated with each organism (within 1 shell height) and number not associated with any organism were recorded.

Four replicate groups of snails were used (designated G1–G4). Each group was tested in three trials, on three consecutive days, using different test organisms each day. Two groups were tested per day. Between experiments the fingerbowl was scrubbed with fresh water and refilled with seawater. Test organisms were washed in fresh water and returned to the bowl. Their positions were haphazardly changed after each experiment to reduce effects of test-organism location on the snails' selection response.

Replicated goodness of fit tests (G-statistic) with William's correction were used to compare the observed distributions of *Odostomia communis* on the five test organisms in each trial with an expected 1:1:1:1:1 null distribution (SOKAL & ROHLF, 1981). In addition, for each trial, data for the four replicate groups were pooled and subdivided to determine which test organisms were responsible for any significant deviation from the null distribution ratio (ZAR, 1984). For all tests a significance level of $\alpha = 0.05$ was used.

RESULTS

Field Investigations

A total of 109 *Odostomia* spp. were examined in the field on 48 pieces of substrata. Of these, approximately 75.2% were associated with serpulid polychaetes, 5.5% were with other encrusting organisms, and 19.3% were not associated with any organism. The mean number of snails associated with serpulids was significantly higher than the number associated with other organisms, or those associated with no organism (non-parametric SNK, $P < 0.01$). An average of only 14.4 ± 14.6% (SD) of the area sampled, however, was covered by serpulid polychaetes, 22.5 ± 19.3% (SD) was covered by other encrusting organisms, and 65.7 ± 26.0% (SD) was free of encrusting organisms. The area covered by serpulids was significantly less than that covered by other organisms, or that which was free of encrusting organisms (SNK, $P < 0.01$).

For all sampled substrata, numbers of *Odostomia* spp. associated with serpulids, other organisms, and no organisms ranged from 0 to 9, 0 to 1, and 0 to 2, respectively. The index of dispersion (I) for snails associated with serpulids was 2.66, and was significantly different from unity ($d = 6.08$; $P < 0.01$), indicating a departure from a random distribution. Because d had a positive value and $s^2 > \bar{x}$, a contagious distribution was suspected. The indices of dispersion (I) for snails associated with other encrusting organisms, and with no organisms were 0.92 and 1.13, re-

spectively. These indices were not significantly different from unity ($d = -0.32$, other organisms; $d = 0.67$, no organism; $P > 0.05$), suggesting a random distribution.

Feeding Observations

Odostomia communis, like most pyramidellids, is a highly motile ectoparasite, frequently moving on and off host and non-host organisms. *Odostomia communis* exhibited three distinct behaviors in connection with host selection.

(1) *Searching*—Snails repeatedly moving towards and away from potential hosts, rotating the shell left and right 180°. Repeatedly everting the proboscis and moving it across the substratum. In some instances perching on the posterior portion of the foot, with the head and tentacles lifted and the proboscis everted and waving back and forth above the head. This behavior usually was exhibited before contacting the soft parts of a potential host.
(2) *Probing*—Snails stationary, the proboscis everted and moving, the oral sucker probing the soft body parts of a potential host.
(3) *Feeding*—Snails stationary, the proboscis everted and the oral sucker gripping the soft body part of a host; buccal pumps vibrating.

Odostomia communis searched for, probed, and fed on serpulid worms most readily. Snails fed on serpulids by attaching their oral sucker to a bipinnate radiole of the worm. Extensive probing of the serpulid radioles usually occurred prior to attachment, and serpulids rarely displayed a strong withdrawal response when parasitic feeding began. Some snails were observed feeding from a single serpulid radiole for as long as 2 h. On several occasions juvenile *Odostomia* spp. (<1 mm in shell height) took up feeding positions on the operculum of serpulids, riding in and out of the calcareous tube when the serpulids retracted and expanded their crown of radioles.

Odostomia communis also searched for, probed, and fed on the bivalves *Isognomon recognitus* and *Arcopsis solida*. In addition, snails were observed searching for and probing the bivalves *Chama echinata* and *Ostrea palmula*; however, no feeding occurred. When searching a gaping bivalve, *Odostomia communis* often everted its proboscis many times along the left and right valve before it could locate the gape and probe the mantle tissue. This search for the mantle tissue of a bivalve took as long as 20 min. Snails were never observed searching for, probing, or feeding on the bivalves *Lithophaga aristata* and *Tellina* sp., or the columbellid and vermetid gastropods, or any tunicates, encrusting sponges, or bryozoans.

Choice Experiments

At the beginning of all experiments *Odostomia communis* moved out from the center of the bowl in all directions. None of the snails appeared to follow a conspecific mucus trail, and many exhibited the searching behavior described earlier. At the end of 11 out of 12 experiments, the highest numbers of *Odostomia communis* were associated with serpulids (Table 1). In one experiment the highest number of snails, and in 5 out of 12 experiments the second highest numbers of snails, were found associated with *Ostrea palmula* (Table 1).

In all trials, the distribution of each of the four groups of *Odostomia communis* was significantly different from the expected even distribution (G-statistic, $P < 0.025$), and all four distributions were heterogeneous with respect to each other (G-statistic, $P < 0.05$). In addition, in each trial the pooled distribution of snails on all test organisms was significantly different from the null distribution (G-statistic, $P < 0.01$). Subdivided pooled distributions, however, indicated that on some test organisms an even distribution of snails did exist. In trials one and two, pooled distributions of snails on *Isognomon recognitus*, *Chama echinata*, and *Arcopsis solida* were not significantly different from the null distribution of 1:1:1 (G-statistic, $P > 0.25$), and in trial three, the pooled distribution of snails on all four bivalve species was not significantly different from the expected null distribution of 1:1:1:1 (G-statistic, $P > 0.25$).

DISCUSSION

Results indicate that *Odostomia communis* predominantly parasitizes serpulid polychaete worms. Like many North American and European pyramidellids, however, this tropical ectoparasite is not host specific and will also feed on two sympatric bivalves, *Isognomon recognitus* and *Arcopsis solida*. Several other pyramidellids, such as *Odostomia lukisii* Jeffreys, *Odostomia unidentata* (Montagu), *Odostomia plicata* (Montagu, 1803) (Fretter & Graham, 1949a; Ankel, 1959), *Fargoa dianthophila* (Wells & Wells, 1961) (Wells & Wells, 1961; Roberge, 1968), and *Fargoa bartschi* (Winkley, 1909) (Robertson, 1978), are known to parasitize serpulid worms.

In the field, the majority of *Odostomia* spp. individuals (75.2%) were consistently associated with serpulids, which covered the least amount of area ($\bar{x} = 14.4\%$). This is in contrast to the significantly fewer *Odostomia* spp. that were associated with other organisms (5.5%) and no organisms (19.3%), which covered significantly greater areas ($\bar{x} = 22.5\%$; $\bar{x} = 65.7\%$, respectively). In addition, the distribution of serpulid-associated snails was contagious. These data indicate that *Odostomia* spp. seek out and aggregate around serpulid polychaete worms. At least one other pyramidellid, *Boonea impressa* (Say, 1822), is contagiously distributed on its predominant host *Crassostrea virginica* (Gmelin, 1791) (White *et al.*, 1984; Powell *et al.*, 1987).

In choice experiments, *Odostomia communis* exhibited a clear preference for serpulid polychaetes over other organisms. In all trials, the highest total numbers of snails were consistently associated with serpulids (Table 1), and group and pooled distributions of snails on test organisms were significantly different from the expected even distri-

Table 1

Number of *Odostomia communis,* in each of the four groups, found associated with test organisms and with no organism at the end of choice-experiment trials. Each group was tested in three trials, on three consecutive days, using different test organisms each day. Groups G1 and G2, $n = 30$; groups G3 and G4, $n = 26$.

	Numbers of associated ectoparasites														
	Trial 1					Trial 2					Trial 3				
Found with	G1	G2	G3	G4	Total	G1	G2	G3	G4	Total	G1	G2	G3	G4	Total
Serpulid polychaetes	9	18	16	13	56	17	16	12	10	55	13	20	15	10	58
Ostrea palmula	11	10	0	4	25	5	2	1	9	17	7	2	2	1	12
Isognomon recognitus	3	0	1	4	8	2	1	0	2	5	0	1	6	4	11
Chama echinata	1	1	2	0	4	3	4	0	1	8	3	1	1	5	10
Arcopsis solida	2	0	1	1	4	1	0	2	0	3	2	2	0	1	5
No organism	4	1	6	4	15	2	7	11	4	24	5	4	2	5	16

bution. Subdivided pooled distributions indicate that the higher numbers of snails on serpulids and *Ostrea palmula* in trials one and two, and the higher numbers on serpulids in trial three, were responsible for the significant deviation from the null distribution. Interestingly, in one experiment the highest number, and in 5 out of 12 experiments the second highest numbers, of snails were associated with *Ostrea palmula* (Table 1); however, snails were never observed feeding on this bivalve, although extensive probing did occur. This finding emphasizes the concerns raised by ROBERTSON & ORR (1961) and ROBERTSON & MAU-LASTOVICKA (1979), that the presence of a pyramidellid with another invertebrate is not sufficient proof that a host–ectoparasite relationship exists.

Probing and feeding behaviors of *Odostomia communis* were similar to those reported for other pyramidellids (FRETTER & GRAHAM, 1949b, 1962; WELLS & WELLS, 1961). However, the searching behavior, of perching on the posterior portion of the foot with the head and tentacles lifted and the proboscis everted above the head, has not been previously reported. This behavior may be a response to dissolved chemicals given off by hosts, and along with rotating 180°, could aid in locating hosts at a distance. Chemoreception is ubiquitous in marine gastropods and is important in numerous interactions, including arousal and orientation to food (as reviewed by KOHN, 1983). The results of this research, as well as several aspects of the biology of pyramidellids such as the reduced osphradium, the highly developed tentacles (FRETTER & GRAHAM, 1949b), and motile behavior, suggest that these snails are adapted for chemolocation of hosts. As *Odostomia communis* moves closer to an organism, the proboscis is repeatedly everted and moved back and forth across the substratum; this behavior could increase the snail's chance of contacting a potential host.

Searching and probing by *Odostomia communis* usually led to feeding, especially when a serpulid host was selected. When a bivalve was selected, however, snails would frequently begin probing, but then stop and abandon their host before any feeding was observed. This occurred most often when *Chama echinata* or *Ostrea palmula* were selected. In addition, snails spent more time searching for the soft parts of bivalves than for the soft parts of serpulids. *Odostomia communis* appeared to have difficulty finding the gape and contacting the mantle tissue of bivalves. Even after parasitic feeding began, if disturbed, snails could not relocate the bivalve's gape without everting their proboscises several times in an apparently haphazard fashion. Another pyramidellid, *Boonea impressa,* which is ectoparasitic predominantly on the oyster *Crassostrea virginica,* was never observed to exhibit this haphazard search for the mantle tissue of its host (WARD, 1985). These observations imply that *Odostomia communis* is less proficient at feeding on bivalves than on serpulids.

In conclusion, the predominant and preferred hosts of *Odostomia communis* are serpulid polychaete worms; however, these snails are not host specific and will also feed on several sympatric bivalves. *Odostomia communis* exhibits a distinct searching behavior that could aid in locating hosts at a distance, and searching and probing behaviors precede and usually lead to feeding. Future research should continue to include field observations, choice experiments, and direct observations of feeding to determine host preferences of tropical pyramidellid snails. In addition, research on the physiological mechanisms and chemicals involved in chemoreception is needed to determine how pyramidellids locate their varied hosts.

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Habitat-Choice Polymorphism Associated with Cryptic Shell-Color Polymorphism in the Limpet *Lottia digitalis*

by

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Abstract. *Lottia digitalis* is a common limpet of the mid- to high-intertidal zone of the Pacific coast of North America. It inhabits rock surfaces, where its shell is typically dark brown or gray in color; it is also common on the plates of the goose barnacle *Pollicipes polymerus,* where its shell is typically white with a pattern of black lines, making it extremely cryptic on this background. In a study on the central Oregon coast, *L. digitalis* living on *Pollicipes* clusters or the surrounding rock were individually marked, moved to the opposite habitat in an unfamiliar area, and observed for up to 12 days. Most limpets of both rock- and *Pollicipes*-type returned to their original habitats, so a true habitat-choice polymorphism exists. This behavioral polymorphism is associated with shell-color polymorphism in a clearly adaptive way. Evidence that selection by bird predators is acting to improve the match between shell color and habitat was obtained. Little evidence that selection is acting on habitat choice was found. Mechanisms for maintaining this adaptive association are discussed.

INTRODUCTION

Lottia digitalis (Rathke, 1833) (=*Collisella digitalis*; see LINDBERG, 1986) is a common limpet of the mid- to high-intertidal zone of the Pacific coast of North America. It has a striking shell-color and pattern polymorphism that has attracted the attention of researchers for at least 40 years (TEST, 1945; GIESEL, 1970; HARTWICK, 1981; LINDBERG, 1981; MERCURIO *et al.,* 1985). Shells of this species range from pure white with no markings to dark brown, gray, or black; most have some dark stripes or patterns on a lighter ground color. Shell color and pattern vary with substratum. Limpets found on the white plates of the goose barnacle *Pollicipes polymerus* are typically white or cream colored with a pattern of black or dark brown lines or chevrons. Their color and pattern make them extremely cryptic on this background. Those found on bare rock are generally much darker and much less conspicuous than light-colored limpets would be.

Visually hunting predators of *Lottia digitalis*—birds such as black oystercatchers, surfbirds, black turnstones, and gulls (FRANK, 1982; GIESEL, 1970; HARTWICK, 1981; LINDBERG, 1981; LINDBERG *et al.,* 1987; MERCURIO *et al.,* 1985) and fish such as surfperch (LINDBERG, 1981; MERCURIO *et al.,* 1985)—may play a role in maintaining this color and pattern polymorphism.

Lottia digitalis exhibits homing behavior (BREEN, 1971; FRANK, 1964, 1965a, 1982; GALBRAITH, 1965; MILLARD, 1968; MILLER, 1968; VILLEE & GROODY, 1940). Experiments capable of distinguishing between homing and habitat choice require habitat reversal of marked individuals in an unfamiliar area (BYERS & MITTON, 1981). GIESEL (1968, 1970) reported that *Pollicipes*-type *L. digitalis* exhibit habitat choice, but his behavioral experiments did not rule out homing by studying habitat reversal in an unfamiliar area.

Experiments described in this report were undertaken to determine whether *Lottia digitalis* exhibits true habitat choice, to examine associations between shell color and habitat choice, and to seek evidence of changes in shell color and/or habitat choice produced by selection. Such experiments may lead to a better understanding of how the adaptive association between cryptic coloration and habitat choice is maintained.

MATERIALS AND METHODS

This study was carried out at Middle Cove, Cape Arago, Oregon (43°19′N, 124°24′W), between 22 July and 3 August 1986. The study site in the southern part of the cove is partially protected from the west and northwest by a

Table 1

Experimental treatment, shell color, and habitat-choice measures by cluster.

	Cluster								
	1	2	3	4	5	6	7	8	9
Tidal height of cluster (m)*	1.6	2.2	2.2	1.9	1.9	1.6	1.6	1.4	1.6
Cluster size (cm^2)	210	397	265	123	99	247	213	144	303
Bird accessibility	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No
Experimental group†	MC	FAM	FAM	UNF	UNF	UNF	UNF	UNF	UNF
Number of limpets‡	32	32	32	28	16	50	50	32	64
Shell length (mm)									
P-type§: mean	9.71	11.50	10.22	10.01	11.11	10.59	10.27	9.86	10.33
SE	0.59	0.47	0.42	0.55	0.77	0.24	0.23	0.13	0.26
R-type: mean	12.45	12.04	10.48	8.99	10.39	11.05	11.94	11.34	10.99
SE	0.67	0.46	0.35	0.59	0.74	0.33	0.46	0.27	0.31
Shell-color score									
P-type: mean	3.81	3.31	3.56	4.07	3.25	3.20	4.04	3.38	4.09
SE	0.44	0.33	0.33	0.45	0.45	0.34	0.27	0.40	0.26
R-type: mean	7.63	7.75	8.06	8.36	8.25	8.24	6.40	6.81	5.97
SE	0.29	0.28	0.17	0.23	0.37	0.27	0.22	0.28	0.24
Days To Return									
P-type: mean	N.A.‖	2.80	3.35	2.00	2.44	2.26	2.66	2.25	2.58
SE		0.37	0.56	0.59	1.12	0.39	0.59	0.51	0.43
R-type: mean	N.A.	3.78	2.84	0.54	0.81	0.96	1.30	1.75	1.53
SE		0.51	0.41	0.33	0.40	0.21	0.31	0.39	0.26
Day 5 Habitat, % return									
P-type	N.A.	40	39	83	60	89	43	93	65
R-type	N.A.	100	100	100	100	95	100	100	100
Final Habitat, % return									
P-type	N.A.	46	67	80	67	92	61	100	81
R-type	N.A.	100	100	100	100	95	100	100	100

* Approximate height, meters above M.L.L.W. (=0.0 m).

† MC = marking control; FAM = familiar-area habitat-reversal, homing control; UNF = unfamiliar-area habitat-reversal, habitat-choice experiment.

‡ One-half of each *n* are *Pollicipes*-type, one-half rock-type; does not apply to habitat-choice measures owing to incomplete recovery of marked limpets.

§ P-type = originally on *Pollicipes*; R-type = originally on rock.

‖ N.A. = not applicable.

rocky reef. The rock substratum at Middle Cove is fine-grained sandstone.

Four pairs of clusters of the barnacle *Pollicipes polymerus* were selected for limpet behavioral experiments. Clusters in each pair were at approximately the same height in the intertidal zone, and at least 3 m from the other cluster of the pair (Table 1). One additional *Pollicipes* cluster was chosen as a control for marking disturbance. Clusters were well defined, and surrounded by large areas of mostly bare rock (Figure 1). Accessibility of each cluster to avian predators of limpets was judged by whether or not there was a vertical surface where a bird could stand within 25 cm of the cluster (FRANK, 1981, 1982).

Limpets from each *Pollicipes* cluster and an equal number from the rock around it were removed from the substratum using a spatula. Limpets from the surrounding rock were chosen arbitrarily, but some attempt was made to choose individuals from the same size range as those found on the *Pollicipes* cluster. In most cases enough limpets were found on the rock within about 30 cm of the cluster to equal the number removed from the cluster. The length of each individual—an indirect measure of age (FRANK, 1965b)—was measured to the nearest 0.1 mm using vernier calipers.

Each limpet's shell color was then scored using a system modified from GIESEL (1970) and HARTWICK (1981). The apex and rim of the shell were scored 0 for white, 1 for gray or grayish brown (or for the rim, also alternating white and dark), and 2 for brown. The shell between the apex and rim was scored 0 for plain white and 6 for solid brown; 1–5 reflected increasing amounts of dark striping on the lighter background of the shell. A total color score

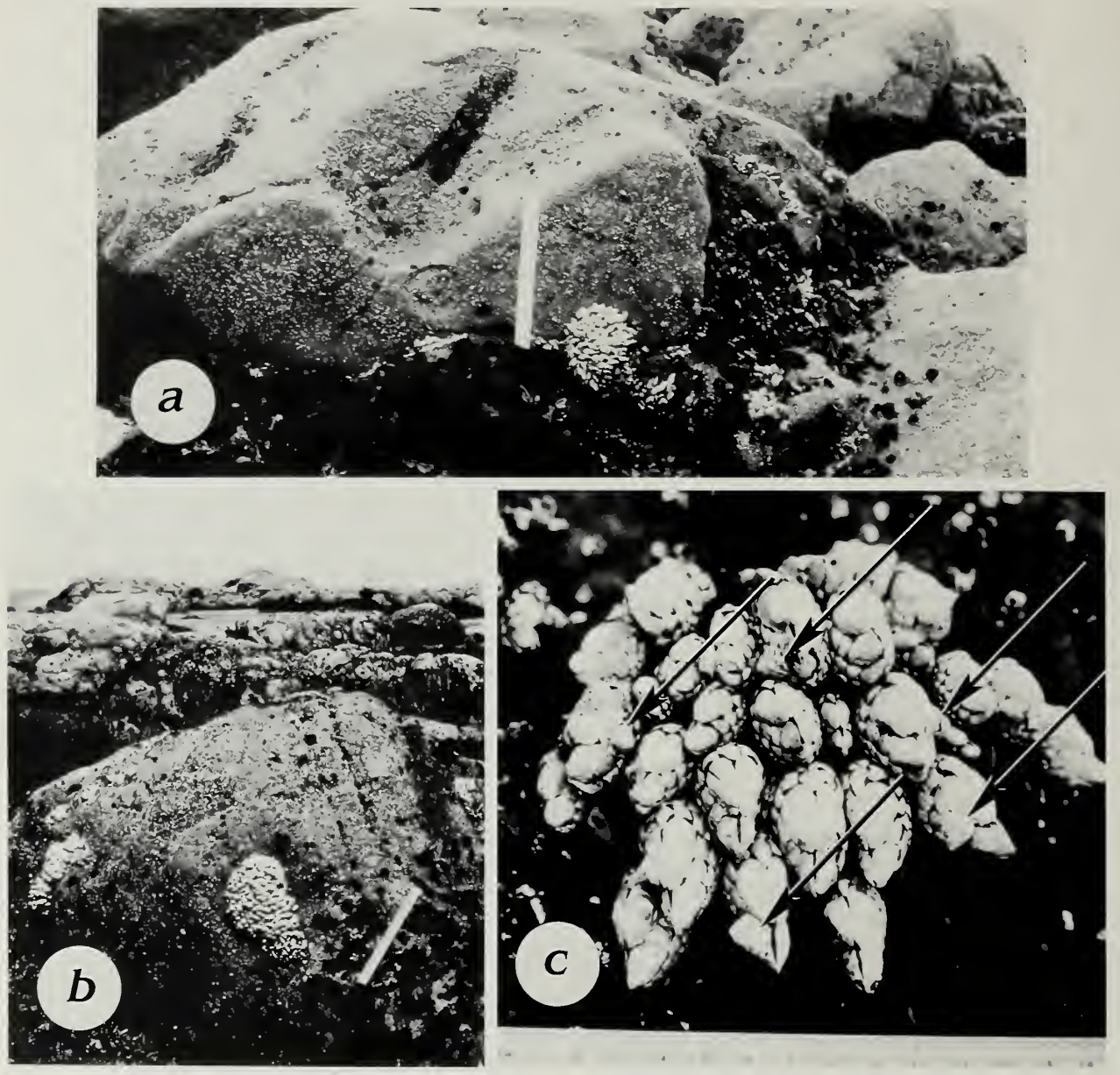

Figure 1

Representative *Pollicipes* clusters used in habitat-choice experiments (see Table 1). a. Cluster 6; ruler in photo is 30 cm long. b. Cluster 9; this cluster, on the vertical side of a large rock, had no horizontal surface within 25 cm where bird predators could stand. c. Cluster 5, with cryptic *Pollicipes*-type limpets (arrows).

was obtained by adding the apex, rim, and striping scores for each individual, such that a score of 0 represented a completely white individual, and a score of 10 a completely dark individual (Figure 2).

After measuring and color scoring each limpet, individually numbered plastic tags made for marking honeybees were glued to each shell with cyanoacrylate ester glue (Superglue®). These numbers are durable in salt water (Byers & Mitton, 1981).

Limpets from on or around Cluster 1, the cluster chosen as a control for disturbance due to removal, handling, and marking, were replaced in their original habitat after disturbance. One pair of clusters, Clusters 2 and 3, was chosen as a control for homing (see Table 1). Limpets originally

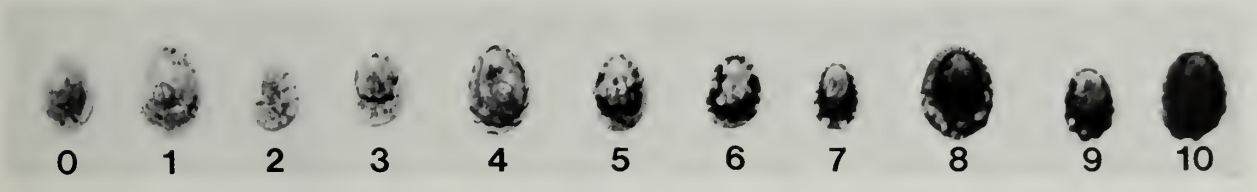

Figure 2

Representative shell colors and color scores (see text for details). Note numbered tags on the shells with scores 1, 4, and 6.

on *Pollicipes* in these two clusters were placed on the rock within 15 cm of their home cluster, and limpets originally on rock around these two clusters were placed on their nearby *Pollicipes* cluster. Three other pairs of clusters were used for habitat-choice experiments. Limpets originally on these *Pollicipes* clusters were placed on the rock within 15 cm of the other cluster of the pair, and thus in a completely unfamiliar habitat at least 3 m away from their home cluster. Limpets originally on rock were placed on the other *Pollicipes* cluster of the pair.

Movement of marked limpets was observed at either the morning or afternoon low tide, and on some days both. Observations were made for at least 5½ and as long as 12 days after marking. Limpets from the different clusters were marked over a period of 6 days at the beginning of the study, so they were observed for different lengths of time after marking. Habitat and position of each marked limpet was recorded as follows: individuals were noted as being on the plates of a *Pollicipes* of their home or foster cluster (the other cluster of the pair in the case of habitat reversal in an unfamiliar area), or on one of three other possible substrata—rock, the shell of a mussel *Mytilus californianus,* or a *Pollicipes* not in the home or foster cluster. If a limpet was not on the home or foster cluster, its distance from the nearest edge of the cluster was measured in centimeters. Approximately 1670 individual positions of 336 marked limpets were recorded.

These individual position records were used to analyze several aspects of habitat choice. The number of days taken to return to the original habitat, "Days To Return," was a quantitative measure obtained for each individual. Two qualitative measures of return to the original habitat also were determined: "Day 5 Habitat" was the substratum (*Pollicipes,* rock, or mussel) of an individual either 5 or 5½ days after experimental manipulation. "Final Habitat" was a qualitative measure of whether a limpet ever returned to its original habitat after experimental reversal. In almost all cases (165/180) once a limpet returned to its original habitat it stayed there, so Final Habitat was usually the habitat on the last day of field observation.

Black oystercatchers were observed in the study area on many occasions, and on 2 August a pair was observed feeding near several study clusters. Sixteen shells of recently eaten rock-type *Lottia digitalis,* none marked, were found approximately 60 cm from one of these clusters. These shells were scored for color.

RESULTS

Shell-Color Polymorphism

The shell-color distributions of limpets from the two habitats were clearly bimodal (Figure 3). *Pollicipes*-type limpets had a mean color score of 3.69 (SD = 1.52) and rock-type limpets had a mean score of 7.29 (SD = 1.45). These means differed significantly ($t = 22.19$, df = 334, $P < 0.001$). The variance of shell color in each group was large, and the two groups overlapped to some extent.

Shell-Color Change with Age and Evidence for Selection

In *Pollicipes*-type limpets (all clusters; $n = 168$) there was a significant regression of shell color on length ($b = -0.152$, SE $b = 0.071$, $F = 4.57$, $P = 0.034$). Larger, and thus older, *Pollicipes*-type limpets were lighter than smaller, younger ones. This relationship was not significant in rock-type *Lottia digitalis* (all clusters; $n = 168$; $b = -0.007$, SE $b = 0.054$, $F = 0.018$, $P = 0.892$).

Color scoring of the shells of 16 rock-type limpets eaten by black oystercatchers allowed a direct test, although with a very small sample, of whether the shell color of limpets eaten by predators differed from the mean color of limpets in the same area. A t-test showed no significant difference between the eaten limpets and the population average.

Comparison of the shell color of limpets from clusters that differed in accessibility to bird predators (Table 1) showed that rock-type limpets found around Cluster 9, the only cluster not accessible to birds, were significantly lighter in color than those from all other clusters ($t = 7.4$, df = 159, $P < 0.001$). No significant shell-color difference between limpets from clusters accessible or not accessible to birds were found in *Pollicipes*-type limpets ($t = 1.80$, df = 159, $P = 0.073$), but limpets from the cluster accessible to birds had the darkest shells of any cluster (Table 1).

Habitat Choice

Limpets showed highly significant return to their original habitats from both familiar-area habitat-reversal ex-

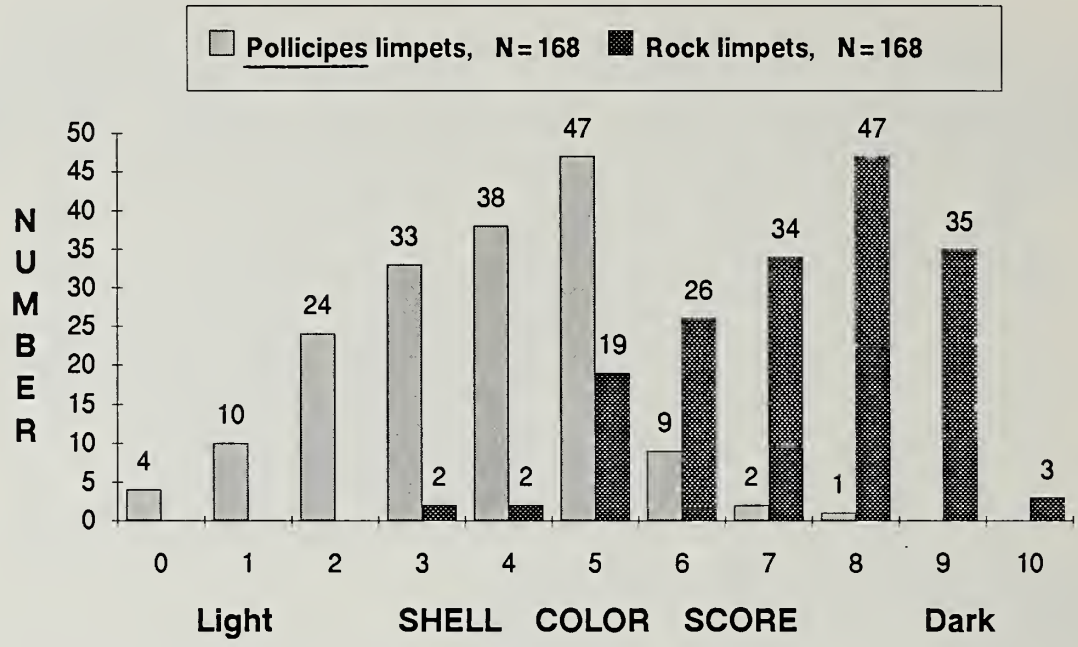

Figure 3

Frequency distribution of the shell-color scores for *Pollicipes*-type and rock-type limpets (n = 336).

periments (Table 2) and unfamiliar-area reversal experiments (Table 3). Limpets in the marking-control cluster, Cluster 1, were not observed in a habitat other than their original habitat.

Pollicipes-type limpets from the two familiar-area habitat-reversal clusters returned to their original habitats at a significantly lower frequency than those from the six unfamiliar-area reversal clusters. This difference was significant both for Day 5 Habitat (χ^2 = 7.40, df = 1, P = 0.007) and Final Habitat (χ^2 = 4.90, df = 1, P = 0.023) measures. Essentially all rock-type limpets from both familiar- and unfamiliar-area reversal experiments returned to their original habitat. Because *Pollicipes*-type limpets from familiar- and unfamiliar-area reversal experiments

Table 2

Habitat choice after experimental reversal in a familiar area.

	Original habitat		
	Pollicipes	Rock	
Day 5 Habitat			
Pollicipes			
%	39.1	0	
n	9	0	
Rock			$\chi^2 = 8.84$
%	60.9	100	df = 1
n	14	23	$P < 0.01$
Final Habitat			
Pollicipes			
%	57.7	0	
n	15	0	
Rock			$\chi^2 = 21.98$
%	42.3	100	df = 1
n	11	32	$P < 0.001$

Table 3

Habitat choice after experimental reversal in an unfamiliar area.

	Original habitat		
	Pollicipes	Rock	
Day 5 Habitat			
Pollicipes			
%	73.0	1.4	
n	54	1	
Rock			$\chi^2 = 74.18$
%	27.0	98.6	df = 1
n	20	68	$P < 0.001$
Final Habitat			
Pollicipes			
%	80.8	1.0	
n	84	1	
Rock			$\chi^2 = 127.51$
%	19.2	99.0	df = 1
n	20	96	$P < 0.001$

differed in habitat choice, all of the following analyses of habitat choice were done using data from the six unfamiliar-area reversal clusters only, in which habitat choice was not confounded with homing.

Tables 2 and 3 show that *Pollicipes*- and rock-type limpets differ in habitat preference, but in order clearly to demonstrate habitat choice by both types of limpets, their observed distributions were compared with distributions expected from random movement in an environment with the proportions of *Pollicipes* and rock substrata found at the study site. The *Pollicipes* clusters used in the study had an average area of 222 cm^2 (see Table 1), and *Pollicipes*-type limpets were placed on rock within 15 cm of a *Pollicipes* cluster in habitat-reversal experiments. In a circle centered on an average cluster and extending 15 cm from its edge, there would therefore be 1498 cm^2 of rock substratum (87% of the total area), and 222 cm^2 of *Pollicipes* substratum (13% of the total area) available to limpets. *G*-tests of independence (SOKAL & ROHLF, 1969) showed that the distributions of both types of limpets differed significantly from expected distributions produced by random movement in an environment with these proportions of available substrata (*Pollicipes*-type, Day 5 Habitat: $G = 57.48$, df = 1, $P < 0.001$; *Pollicipes*-type, Final Habitat: $G = 103.66$, df = 1, $P < 0.001$; rock-type, Day 5 Habitat: $G = 7.86$, df = 1, $P < 0.01$; rock-type, Final Habitat: $G = 13.00$, df = 1, $P < 0.001$).

Pollicipes- and rock-type limpets differed significantly in Days To Return, the speed of return to their original habitat. Rock-type limpets returned to their original habitat with a mean of 1.22 days (SD = 1.41, $n = 120$), and *Pollicipes*-type limpets with a mean of 2.41 days (SD = 2.39, $n = 120$). The variance of Days To Return differed significantly between these two groups ($F = 2.89$, $P < 0.001$), but sine-transformed data had equal variances, and a *t*-test on these transformed data also revealed a highly significant difference between means ($t = 3.99$, df = 238, $P < 0.001$).

Pollicipes-type limpets were much more likely to be found on rock than rock-type limpets were to be found on *Pollicipes*. Fifteen of the 120 *Pollicipes*-type limpets shifted to rock after returning to *Pollicipes*, whereas none of the 120 rock-type limpets shifted to *Pollicipes* after returning to rock. The percentage of all position records (after Day 0, the day of reversal) of *Pollicipes*-type limpets on rock was 19.3% (134/694 records); for rock-type limpets on *Pollicipes* this percentage was 7.0% (39/556 records). A *G*-test of independence showed this to be a highly significant difference ($G = 767.0$, df = 1, $P < 0.001$). The percentage of individuals in each group that ever used the opposite habitat as a substratum (after Day 0) were 66.6% (80/120) of *Pollicipes*-type limpets and 21.6% (26/120) of rock-type limpets. This difference was highly significant ($G = 51.23$, df = 1, $P < 0.001$).

Behavioral data also revealed that rock- and *Pollicipes*-type limpets differed in their use of mussels as alternative substrata. Sixteen of the 120 *Pollicipes*-type limpets shifted to mussels after returning to *Pollicipes*, whereas only one of the 120 rock-type limpets shifted to mussels after returning to rock. The percentage of all position records (after Day 0) of *Pollicipes*-type limpets on mussels was 8.9% (62/694 records); for rock-type limpets this percentage was 1.6% (9/556 records). This difference was highly significant ($G = 35.31$, df = 1, $P < 0.001$). This measure may be biased by mussel-prone individuals; the 62 records for *Pollicipes*-type limpets, for example, were among only 35 individuals. A way to overcome this bias is to compare the percentage of individuals in the two groups that ever used mussels as a substratum: 29.2% (35/120) of *Pollicipes*-type and 6.7% (8/120) of rock-type limpets used mussels, a highly significant difference ($G = 22.00$, df = 1, $P < 0.001$).

Habitat-Choice Change with Age and Evidence for Selection

To test the hypothesis that the habitat-choice behavior of the limpet population changes within a generation, Days to Return was regressed against shell length, an indirect measure of age. This regression was not significant for either *Pollicipes*-type ($b = -0.119$, SE $b = 0.155$, $F = 0.592$, $P = 0.443$) or rock-type limpets ($b = 0.035$, SE $b = 0.065$, $F = 0.286$, $P = 0.594$).

Similarly, no differences in shell length were observed between limpets that returned or did not return for Final Habitat in either *Pollicipes*- or rock-type limpets. A significant difference in lengths was observed, however, between *Pollicipes*-type limpets that returned or did not return by Day 5 ($t = 2.27$, df = 71, $P = 0.026$); limpets that did not return were significantly larger than those that did. No such difference was observed for rock-type limpets.

Partial correlation analysis revealed a significant partial correlation in rock-type limpets between shell color and Days To Return when length was controlled ($r = -0.184$, df = 117, $P = 0.023$): darker rock-type limpets returned to rock faster than lighter ones did. No such correlation was observed in *Pollicipes*-type limpets ($r = -0.058$, df = 117, $P = 0.267$), however.

Because virtually all rock-type limpets returned to their original rock habitat, comparisons of shell color between returnees and non-returnees were not meaningful. Among *Pollicipes*-type limpets, which returned to their original habitat less frequently, *t*-tests showed no significant differences in shell color of returnees versus non-returnees for either Day 5 Habitat ($t = 0.75$, df = 71, $P = 0.455$) or Final Habitat ($t = 1.31$, df = 102, $P = 0.192$).

Chi-squared tests showed no differences between either *Pollicipes*- or rock-type limpets from clusters accessible or inaccessible to birds in either Day 5 Habitat or Final Habitat. Hence, bird predation did not appear to be acting as a selective agent to change behavior.

DISCUSSION

Shell-Color Selection

The shell-color polymorphism observed here in *Lottia digitalis* has been reported in other studies (GIESEL, 1970; HARTWICK, 1981). If predation were responsible for this polymorphism, the frequency of cryptic limpets on each substratum should increase with age, as predators remove the more conspicuous individuals. Larger, and presumably older, *Pollicipes*-type limpets in this study were lighter, as predicted by the shell-color selection hypothesis. However, shell color may also become lighter with age because of diet or infection by shell-eroding fungus. The latter might be especially important for *Pollicipes*-type limpets, because the barnacles may provide a source of fungal infection (D. Lindberg, pers. comm.).

Shell color did not vary with shell length in rock-type limpets, contrary to the prediction of the selection hypothesis, although GIESEL (1970) did report such a correlation in a population of very small (3.0–5.9 mm) rock-type limpets.

HOAGLAND (1977) found that matching with a cryptic substratum improved with age in the gastropod *Crepidula convexa,* and HUGHES & MATHER (1986) found age-related changes in the shell colors of *Littorina* sp. living on mangroves. Predation was proposed as the cause of the shell-color changes in both studies.

The significantly lighter shell color of rock-type limpets found around the only *Pollicipes* cluster in this study that was inaccessible to bird predators suggests that bird predation affects the distribution of shell color. Avian predators appear to affect the frequency of cryptic morphs of the limpet *Scurria variabilis* in central Chile (HOCKEY *et al.,* 1987).

The rock-type limpets eaten by black oystercatchers in this study were not significantly different in color from the rest of the population. HARTWICK (1981) studied shell-color selection by black oystercatchers in limpets placed in artificial arrays in the field. The rock-type *Lottia digitalis* eaten from these arrays appear to be lighter than those in the surrounding rock-type population (HARTWICK, 1981: compare figs. 6 and 8b), as predicted by the shell-color selection hypothesis.

MERCURIO *et al.* (1985) conducted field experiments that revealed that light-colored limpets disappeared more rapidly from dark-colored mussels than from the light-colored barnacles after exposure to predation by surfperch. In addition, after exposure to bird predation, significantly more limpets disappeared from barnacles than from mussels, an unexpected result; but significantly fewer light-colored *Lottia digitalis* than dark-colored *L. pelta* (Rathke, 1833) disappeared from the barnacle substratum. The disappearance rates due to predation reported in the study by MERCURIO *et al.* (1985) are remarkably high. About 17% of *L. digitalis* on the barnacle substratum and 54% on the mussel substratum disappeared after exposure to surfperch predation during only one high tide; about 10–20% disappeared after exposure to bird predation during one low tide. These high rates of predation suggest that selection by visually hunting predators could be strong.

REIMCHEN (1979) observed differential predation by blennies on two shell-color morphs of *Littorina mariae* that occupied two different habitats; in each of which one of the morphs was cryptic.

Shell color in archaeogastropods may be affected by environmental factors, especially diet (ROBERTSON, 1985). Shell color and pattern in species of other gastropod orders has been shown to be genetically determined (CAIN & SHEPPARD, 1954; KOMAI & EMURA, 1955; PALMER, 1984, 1985; REIMCHEN, 1979). GIESEL (1970) concluded that genetic factors were the major determinant of shell color in *Lottia digitalis,* but that color could also be modified by environmental factors. Laboratory studies by D. Lindberg and J. Pearse (D. R. Lindberg, pers. comm.) suggest that shell color in this species can be modified by diet.

Habitat Choice versus Homing

Habitat choice could play a major role in maintaining a polymorphism such as the shell-color polymorphism in this species, according to theoretical models (HEDRICK *et al.,* 1976; POWELL & TAYLOR, 1979). GIESEL (1968, 1970) reported that *Pollicipes*-type *Lottia digitalis* exhibit habitat choice. *Lottia digitalis* is known to home, however, and because Giesel's study did not include habitat reversal in an unfamiliar area, homing and habitat choice were confounded.

The results presented above conclusively demonstrate that *Lottia digitalis* has a habitat-choice polymorphism. Both *Pollicipes*-type and rock-type limpets whose habitats were reversed in an unfamiliar area showed significant return to their original habitat. Whereas rock-type limpets exhibit virtually complete fidelity to rock, not all *Pollicipes*-type limpets return to *Pollicipes*. Because the area of rock in the vicinity of an isolated *Pollicipes* cluster is much greater than the area of the cluster, the fact that most *Pollicipes*-type limpets do return to *Pollicipes* is evidence of a strong habitat preference. The slower and less complete return by *Pollicipes*-type limpets may result from the greater difficulty of finding a small, isolated *Pollicipes* cluster in a large expanse of rock.

Rather unexpectedly, *Pollicipes*-type limpets whose habitats were reversed in a familiar area returned at a significantly lower frequency than those in an unfamiliar area. A combination of homing and habitat choice in the familiar-area reversal groups should have led to a greater return frequency than habitat choice alone in the unfamiliar-area reversal groups. This difference in return rates may be due to subtle and unrecognized ecological differences between the two familiar-area reversal clusters and the six unfamiliar-area reversal clusters. It could also be that limpets are somewhat familiar with local topography, and if they are displaced and recognize some cues, they

try to return home; however, if they are displaced to a totally unfamiliar area, they switch behavioral modes and make use of habitat choice to find the nearest *Pollicipes* cluster. At the least, this result suggests that homing is not overwhelmingly strong.

Natural Selection for Habitat Choice

Because habitat choice is adaptively associated with shell color, the selection hypothesis would predict that differential predation would also act to improve this behavior. However, no evidence of selection acting directly on habitat choice was found: the frequency of returnees did not increase with increasing size, and none of the habitat-choice measures differed between bird-accessible and bird-inaccessible clusters.

Partial correlation analysis did show a significant correlation in rock-type limpets between shell color and Days To Return when length was controlled, however. The negative correlation coefficient ($r = -0.184$) indicates that lighter rock-type limpets, which are presumably less cryptic on rock and more cryptic on *Pollicipes,* take significantly longer to return from *Pollicipes* to rock, as predicted if selection has acted to create a correlation from an initially independent distribution of shell color and behavior. In *Pollicipes*-type limpets there was no significant partial correlation between color and Days To Return when length was controlled. GIESEL (1968, 1970) reported that shell color and return time are correlated in small (<8 mm) *Pollicipes*-type limpets.

Habitat choice may be heritable, but evidence is lacking and would be difficult to obtain. Evidence for a genetic correlation between habitat choice and a fitness-related character in an insect was reported by VIA (1986). The kind of rigorous genetic analysis required to demonstrate genetic covariance between shell color and habitat choice probably would be impossible in *Lottia digitalis,* which spawns and has planktonic larvae (FRITCHMAN, 1961; GEISEL, 1970; MERCURIO *et al.,* 1985).

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Air Pockets: A Subtidal Habitat for the Intertidal Marine Pulmonate Limpet *Trimusculus reticulatus*

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Abstract. Subtidal air pockets were found to serve as a unique habitat for the intertidal pulmonate limpet *Trimusculus reticulatus*. Observations indicated that the bubbles, discovered on the underside of a ledge approximately 3.5 m deep, arise naturally from air suspended by wave action at high tide. The air-breathing limpets remain sedentary and feed at irregular intervals when the volume of the bubbles decreases sufficiently to immerse them.

INTRODUCTION

During SCUBA diving trips to the reefs of Laguna Beach, California, I noticed pockets of air trapped beneath rock ledges. In subsequent surveys, I found air-breathing limpets of the species *Trimusculus reticulatus* (Sowerby, 1835) occupying many of the bubbles. To my knowledge, there have been no prior studies of such pockets, or of organisms living in this unique microhabitat.

RICE (1985), BEEMAN & WILLIAMS (1980), and YONGE (1958) reported that *Trimusculus reticulatus* is found in the intertidal zone along the west coast of North America. The limpet, which can breathe in air and under water, usually lives clustered in dense colonies on the roofs of caves. WALSBY (1975) showed that, although it retains the ability to move in unnatural situations, *Trimusculus* is essentially sessile. The animal feeds while remaining stationary by secreting a mucus net in which it traps water-borne particles.

Subtidal air pockets, although previously noticed by divers, have not been investigated from an ecological point of view. This study examines the origins of the air pockets and how they serve as a subtidal habitat for a normally intertidal pulmonate limpet.

STUDY SITE

Observations were made in a surge channel that cuts through a rock reef at Shaw's Cove in Laguna Beach, California (33°33′N, 117°48′W). The average depth of the channel is 15 feet (4.5 m), and the width varies from 0.75 m at the narrowest to approximately 4 m at the broadest. At low tide the channel is protected from direct wave action by an outer reef, but at high tide the reef is inundated by 0.3 to 0.6 m of water. The resulting turbulence fills the channel with air bubbles, often all the way to the bottom. The current from a turbulent intersecting cross-channel augments this aeration (Figure 1).

The ledge where the air pockets are found is directly beneath the narrowest part of the main channel and is a result of dramatic widening near the bottom (Figure 2). This overhang is at an average depth of 11 feet (3.4 m). It is approximately 2 m long from its edge to its furthest recesses and 0.5 to 0.75 m above the floor of the channel.

MATERIALS AND METHODS

Observations were made between 5 March and 10 April 1988, by snorkeling, so that the air bubbles were not affected. Depths were measured to the nearest foot using a Dacor depth gauge. The volume of a pocket was measured underwater by removing the air from the cavity with a syringe and emptying it into an inverted graduated cylinder, thus displacing the water. After the volume was read, the air was carefully returned to its original location so that the sampling was relatively non-destructive. Values reported are the volumes of air measured at the depth of the pocket, not at the surface.

To determine whether the bubbles received a significant contribution from the exhalations of SCUBA divers, gas chromatography was performed using a Varian aerograph, model 90-P, using a Porapak column. Air was transferred from a pocket to a sample tube using a 10-mL syringe. Purity of air samples was ensured by performing the transfer completely beneath the surface of the water.

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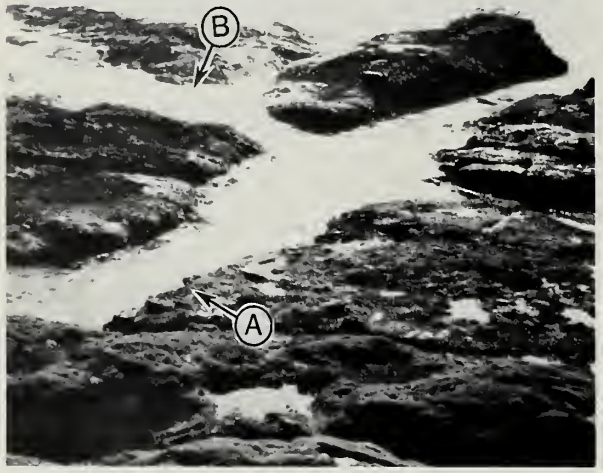

Figure 1

The channel at a +1 foot (+0.3 m) tide. A. The narrowest part of the channel where the cross-section shown in Figure 2 is taken. B. The intersecting channel that provides air to the main channel.

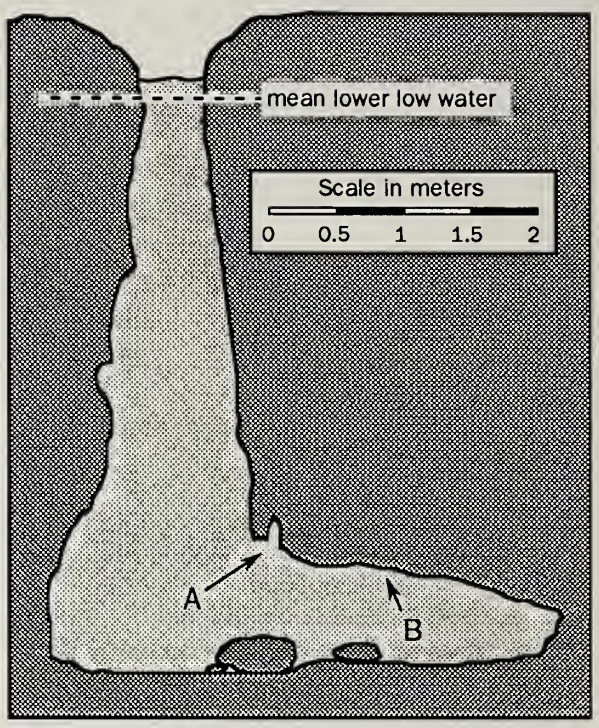

Figure 2

A schematic cross-section of the channel. A. The crack where the two largest air pockets occur. B. The overhang, which is often covered with small bubbles.

To confirm that the limpets remained stationary in the subtidal habitat, I selected three limpets that were completely out of the water in separate air pockets. A mark was made on the rock next to each limpet in line with a mark on the animal's shell, so that if the limpet changed location or orientation it would be apparent. One week later the limpets were rechecked.

RESULTS

Trapped beneath the ledge were a few dozen small bubbles (2.5 cm diameter, 10 mL volume), a few mid-sized bubbles (4 × 5 cm, 25 mL), and three large bubbles that averaged more than 250 mL (10 × 12 cm to 12 × 25 cm). The two largest bubbles were trapped in a deep crack on the edge of the overhang (Figure 2). Many small bubbles were observed along the underside of the ledge to its furthest recesses. The largest bubbles were not displaced about their periphery more than 1 cm by the surge, and the volume changes due to pressure differences between high and low tide were calculated to be less than 15%.

The results of the gas chromatography were inconclusive. The CO_2 levels of the bubbles were low—roughly between 0% and 0.5%—but at such levels, the method of measurement is imprecise. For comparison, atmospheric air contains approximately 0.035% CO_2, and a normal human exhalation contains 3–3.5%.

Tests in which pockets were emptied to observe the refill rate were unsuccessful because of an inability to return to the study site with sufficient frequency. On some occasions, pockets that had been emptied were found filled a week later; at other times pockets that had been full were found with less air in them. It was not possible to correlate these changes with other factors such as surf conditions, tidal levels, or the presence of divers. On one occasion, however, two sets of SCUBA divers passed next to the ledge shortly after a large pocket had been emptied. When both groups (a total of nine divers) had passed, the emptied pocket was rechecked, and the amount of air within it had not increased noticeably.

During one dive I noted that many of the limpets in a large pocket were attached several centimeters within the edge of the air bubble. Two weeks later the bubble was approximately half its previous size, and all of the limpets, including those formerly well within the edge of the bubble, were exposed to the water. The portion of rock that was still covered by air appeared completely barren. This seems to indicate a minimum size to the bubble that prevents any marine organism from settling.

Within the bubbles were found limpets (*Trimusculus reticulatus*), a few barnacles (*Balanus glandula*), and, on one occasion, a snail (*Ceratostoma nuttallii*). Spirorbid worms were frequently found on the backs of the limpets. In contrast, the areas immediately surrounding the pockets were inhabited by tube worms (*Serpulorbis* sp.) and sea

urchins (both *Strongylocentrotus purpuratus* and *S. franciscanus*) and encrusted with various sponges.

Trimusculus was found in large numbers in pockets of all sizes. Bubbles with only 10 mL of air could contain as many as 4 or 5 limpets clustered together, a mid-sized pocket might contain 8, and the largest pocket had within it a colony of 61 limpets. Limpets collected ranged in size from 1.2 cm to 1.7 cm in diameter.

The limpets were found in tight aggregations, and the edges of their shells were often convoluted in close conformity with the irregular rock surface. One empty shell was attached firmly to the reef by a worm's tube. In the experiment in which marks were made on limpets and on the adjoining rock, all three limpets were found in the same position and orientation one week later.

DISCUSSION AND CONCLUSIONS

In an intertidal environment, *Trimusculus reticulatus* is exposed alternately to air, where it can breathe but not feed, and water, where it can feed. Because it does not graze, but "filter feeds" by secreting mucus (WALSBY, 1975), a limpet living in an air pocket must be exposed to the water at regular intervals. This study indicates that, in this subtidal environment, alternating periods of exposure to air and water are a result of natural changes in bubble size: there is no indication that subtidal *Trimusculus* deviates from the sedentary behavior reported for intertidal populations.

The results of this study suggest the following explanation for the origin of the air pockets. When the tide is sufficiently high (about +0.6 m, depending on the size of the surf), waves crashing over the rocks fill the water in the channel with tiny bubbles. The surge also brings in aerated water from the turbulent intersecting channel. As this air collects in the nooks of the ledge and in the deep cavities of the crack, the bubbles gradually grow. The bubbles diminish during low tides, when the current in the channel draws air from the large pockets. In some hollows, air may also seep slowly through the rock. The amount of air in the pockets changes gradually, however, remaining fairly constant over the short term.

YONGE (1958) suggested that the limpet's ability to breathe air may be the key to its survival in the face of intertidal competition. Similarly, in the subtidal habitat this trait allows *Trimusculus reticulatus* to take advantage of a refuge that is ostensibly quite different from the limpet's intertidal habitat. If nothing else, this unique situation reminds us to keep our eyes open for unexpected solutions to the demands placed on organisms by nature.

ACKNOWLEDGMENTS

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First Tertiary Occurrence of a Rare Patelliform Gastropod (Archaeogastropoda: Symmetrocapulidae), Eocene Tejon Formation, Tehachapi Mountains, California

by

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Abstract. Two specimens of ?*Symmetrocapulus* sp., a moderately large patelliform gastropod, were found in rocky nearshore deposits of the middle Eocene Tejon Formation, western Tehachapi Mountains, at the southern end of the Great Valley of California. This rare genus, which is provisionally classified in the Archaeogastropoda, has been previously known only from Jurassic through Lower Cretaceous deposits in Europe, Africa, and Japan. The Tejon specimens extend the geologic range of this rare genus into the middle Eocene and extend its geographic range into the Western Hemisphere.

INTRODUCTION

Two moderately large and very rare specimens of the patelliform gastropod ?*Symmetrocapulus* sp. were recently found by the author while intensively collecting middle Eocene rocky nearshore deposits in the basal part of the marine Tejon Formation, western Tehachapi Mountains, south-central California. The shell apex of each specimen is posterior; the asymmetrical horseshoe-shaped muscle scar is posterior and very high dorsally. *Symmetrocapulus* has been previously known only from Jurassic through Lower Cretaceous deposits in Europe, Africa, and Japan (KASE, 1984).

Abbreviations used for catalog and/or locality numbers are: CSUN, California State University, Northridge; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section.

MATERIALS

Two specimens of ?*Symmetrocapulus* sp. were found at locality CSUN 1201, 13 m above the base of the Tejon Formation, in a steep-sided roadcut exposure about 20 m east of the eastern side of the Edmonston Pumping Plant, 16 km east of Grapevine, Kern County, California. The exposures at the pumping plant are predominantly sandstone and are badly weathered and crumbly. Fossils are poorly preserved and chalky. Only the inner shell layer is present in the two ?*Symmetrocapulus* specimens. The muscle-scar pattern is also present in both specimens. A partial external mold of one of the specimens (hypotype, LACMIP 8048) was found, but the thin outer shell layer is inseparably fused to the surrounding rock matrix. On this specimen, the innermost surface of this outer shell layer is smooth with numerous algal or sponge boreholes. No characters of external shell features were discernible.

The Tejon specimens are compared to casts of the European *Symmetrocapulus tessoni* (J. A. Eudes-Deslongchamps, 1843), and to casts of the Japanese *S. hanaii* Kase, 1984. All these casts were provided by Tomoki Kase of the National Science Museum, Tokyo, Japan. Comparisons were also made with illustrated specimens in the literature.

DEPOSITIONAL ENVIRONMENT AND GEOLOGIC AGE

The ?*Symmetrocapulus* specimens were collected from an abundantly fossiliferous lens at locality CSUN 1201. This lens was part of a shoreline-associated sequence of rocky nearshore deposits that was laid down as a transgressing sea advanced over an irregular surface of gneissic bedrock during the middle Eocene ("Transition Stage") (SQUIRES, 1989a, b; LINDBERG & SQUIRES, in press). The 1-m-

Explanation of Figures 1 to 3

Figures 1 to 3. *?Symmetrocapulus* sp., dorsal, left lateral, and posterior views of hypotype, LACMIP 8048, locality CSUN 1201.

Figures 1 and 2: ×1.1. Figure 3: ×1.3.

thick lens represents a poorly sorted, channel-lag storm accumulation of marine molluscan debris indicative of a rocky nearshore environment. The bivalves *Acustostrea, Anomia, Brachidontes,* and, especially, *Isognomon* are abundant. The *Isognomon* from this lens is discussed in SQUIRES (1989b). Patellogastropod limpets from this lens and associated lenses are described in LINDBERG & SQUIRES (in press).

SYSTEMATIC PALEONTOLOGY

Family SYMMETROCAPULIDAE Wenz, 1938

Genus *Symmetrocapulus* Dacqué, 1933

Type species: By original designation, *Patella rugosus* J. Sowerby, 1816 (*non* Röding, 1798), Middle Jurassic (Bathonian), England.

?*Symmetrocapulus* sp.

(Figures 1–3)

Description: Shell moderately large. Hypotype, LACMIP 8048, length 72 mm, width 63 mm; hypotype, LACMIP 8049, length 74 mm, width 50 mm (incomplete). Very low profile patelliform shell. External shell layer thin and prismatic? Internal shell layer thicker and nacreous lamellar with a nonnacreous, crossed-lamellar muscle scar. Dorsally situated, horseshoe-shaped muscle scar broadly open anteriorly. Left arm of muscle scar longer and less sharply curved than the right. Scar narrowest at posterior end. Scar rising anteriorly. Apex about ⅓ of maximum length from posterior end. Posterior slope concave. Anterior slope convex. Exterior features not known, but closely spaced concentric ribbing seems to be present just posterior to the apex.

Discussion: The familial placement of *Symmetrocapulus* has long been uncertain. COX (1960) followed WENZ (1938) in retaining *Symmetrocapulus* in the superfamily Patellacea, but COX (1960) elevated Wenz's subfamily to the queried family Symmetrocapulidae. COX (1960) mentioned that this family may eventually prove to be related to the mesogastropod family Capulidae.

KASE (1984) transferred *Symmetrocapulus* to the family Capulidae, based on the characters of the muscle scar and the posteriorly situated shell apex. MCLEAN (1988) rejected this familial assignment, and, based on the horseshoe-shaped muscle scar and posterior apex in which the first teleoconch whorl is coiled and offset to the right, provisionally ranked Symmetrocapulidae as a sister group to the smaller sized, deep-sea hydrothermal-vent limpets in the Lepetrodilacea and the "tapersnout" limpets, which

were subsequently described in the Peltospiracea (McLean, 1989). McLean (1988) hypothesized that these hydrothermal-vent archaeogastropod limpets are living derivatives of families, like Symmetrocapulidae, that once were distributed more broadly in the shallow seas of the Late Paleozoic and Mesozoic. With this new occurrence of ?*Symmetrocapulus* sp. in middle Eocene rocky nearshore deposits, the fossil record of the possible ancestors of the modern hydrothermal-vent limpets can now be extended into the early Cenozoic. Members of *Symmetrocapulus* inhabited wave-swept rocky coasts, but this habitat is poorly represented in the fossil record because taxa from this high-energy environment rarely survive taphonomic processes intact.

?*Symmetrocapulus* sp. from the Tejon Formation is questionably placed in genus *Symmetrocapulus* because poor preservation prevents positive assignment. If the Tejon specimens are true *Symmetrocapulus,* then erosion of the shell has completely obliterated the offset, asymmetrical apex that is a diagnostic feature of this genus, as shown in the figures for the type species of the genus in Cox (1960:fig. 144a, b). What is called the protoconch in the description therein is evidently the first teleoconch whorl (McLean, 1989; pers. comm.). If future specimens of ?*Symmetrocapulus* sp., however, reveal that the asymmetrical apex is truly not present, then this species would be similar to the European *S. tessoni* (J. A. Eudes-Deslongchamps, 1843:113–114, pl. 7, figs. 3, 4) and the Japanese *S. hanaii* (Kase, 1984:149, pl. 24, figs. 5–7). It may be that these three belong in an undescribed genus of Symmetrocapulidae, one in which the coiled first teleoconch whorl is lost and the progression to bilateral symmetry is more complete than in true *Symmetrocapulus.*

?*Symmetrocapulus* sp. from the Tejon Formation resembles *Symmetrocapulus hanaii* (Kase, 1984:149, pl. 24, figs. 5–7) in characters of size, shape, posterior apex, muscle scar, and asymmetry of the arms of the muscle scar. *Symmetrocapulus hanaii* is known from Lower Cretaceous deposits in Japan (Kase, 1984). The middle Eocene ?*Symmetrocapulus* sp. from the Tejon Formation is the only known Tertiary species of *Symmetrocapulus* and the only species known from the Western Hemisphere. The Tejon specimens of ?*Symmetrocapulus* sp. most likely represent a new species because of its disparity in geologic age and geographic position with *S. hanaii,* but a new species cannot be diagnosed at this time owing to the lack of exterior features.

Sohl (1965:15, pl. 1, figs. 22–24) reported a single specimen of ?*Symmetrocapulus corrugatus* Sohl, 1965, from the lower limey part of the Middle Jurassic (Bajocian) Carmel Formation, central Utah. He was unable positively to assign this specimen to *Symmetrocapulus* because the muscle-scar pattern was not known.

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NOTES, INFORMATION & NEWS

Embryology and Larval Development of *Haminoea vesicula* Gould (Opisthobranchia: Cephalaspidea)

by
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Introduction

Large populations of *Haminoea vesicula* Gould, 1855, are common in muddy bays and eel grass beds along the northeastern Pacific coast (MORRIS *et al.*, 1980). However, the development of this species has not been described, with the exception of observations of early cleavage stages (LEONARD, 1918) and synchrony of embryological development within an egg mass (CHAFFEE & STRATHMANN, 1984). The high fecundity of this planktotrophic species suggests that *H. vesicula* veligers potentially constitute a large proportion of the planktonic community within adult-inhabited bays. In this note, we present a brief description of the embryology and larval and juvenile development of *H. vesicula*.

Materials and Methods

Adults and egg masses were collected from Grappler and Bamfield Inlets, Barkley Sound, British Columbia, Canada, periodically from May 1985 to July 1986. Adults were maintained in glass aquaria with a continuous flow of seawater at seawater-table temperatures (12–15°C), and supplied with *Zostera marina* and *Ulva* sp. as food.

Egg masses were collected immediately after oviposition and maintained in Pyrex dishes. Culture water was replaced daily with 1-μm filtered seawater. Flakes of cetyl alcohol were added to each culture one day prior to the onset of hatching to prevent the veliger shells from being caught in the surface tension (HURST, 1967). Hatched veligers were removed daily and cultured as described by KEMPF & WILLOWS (1977), at concentrations of 0.8 veligers/mL. Larvae fed a 1:1 mixture of *Isochrysis galbana* (Tahitian strain) and *Pavlova lutheri* (at concentrations of 10^5 cells/mL) showed the greatest growth and survival rates, although, in the laboratory, veligers would also ingest *Cyclotella cryptica*, *Dunaliella* sp., *Tetraselmis* sp., and *Thallossiosira* sp. Veliger growth was determined according to HURST (1967) in 10 individuals in each of 10 cultures every second day.

Attempts were made to induce metamorphosis in competent veligers. Veligers were identified as being competent when they showed a well-developed propodium, maximum shell growth (length 180 μm, depth 130 μm), behavioral changes such as swimming at the bottom of the culture

Table 1

Summary of developmental events in *Haminoea vesicula* Gould from oviposition to metamorphic competence. Time is listed in hours (h) and days (d; 12–15°C).

Time (h, d)	Developmental event
0 h	—oviposition
10 h	—1st cleavage (holoblastic and equal)
13 h	—2nd cleavage (holoblastic and equal)
23 h	—blastula
26–35 h	—gastrula
3.5 d	—prototroch, embryos irregularly rotating in capsules
4 d	—flat cephalopedal rudiment visible, embryos rotating regularly, invagination of shell gland visible
4.5 d	—shell growth evident, velar and pedal rudiments distinct
5.5 d	—velum bilobed, shell growth over posterior half of yolk mass
6 d	—metachronic beating of cilia; larval shell has grown to base of velum; further shell growth not evident until after hatching
7 d	—yolk decreased, larval gut rudiments visible
8 d	—stomach and intestine visible, digestive glands still yolky, red nephrocyst apparent
8.5 d	—larval retractor muscles functional, intestine connects with mantle cavity
9–12 d	—hatching —morphology similar to other planktotrophic veligers, distinguished by bright red larval kidney; newly hatched veligers with a shell length of 123 ± 12 μm (comprising ¾ of a whorl), shell type 1 (THOMPSON, 1961) —yolk reserves finished and unicellular algae visible in the stomach 2–3 d post-hatching, veligers actively swimming
17 d	—stomach and left digestive gland enlarged, left digestive gland curved ventrally over the stomach to reach the larval right, shell length 146 ± 12 μm —high mortality at 18–21 d (9–12 d post-hatching)
24 d	—nephrocyst darker red in color, metapodium thicker, shell length 156 ± 9 μm —veligers actively swimming high in culture dishes
31 d	—anterior metapodium thicker, eyespots visible, nephrocyst darker and eventually turning black, shell length 160 ± 23.4 μm —high mortality at 27–33 d (18–24 d post-hatching)
40–45 d	—veligers competent to metamorphose; *i.e.*, with well-developed propodium, and maximum shell size (180 ± 11.25 μm; 1.5 turns in whorl); mantle did not withdraw from shell aperture —veligers swimming near bottom of culture dish (THOMPSON'S, 1958, "searching" behavior), velar lobes fully extended

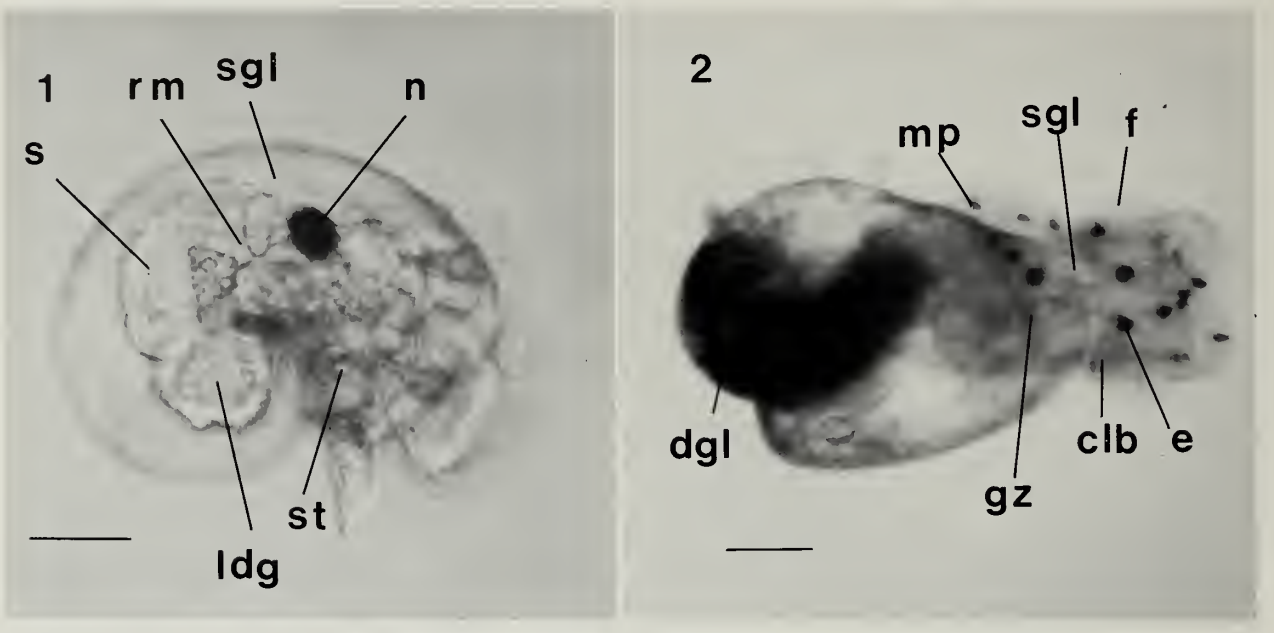

Figure 1

Haminoea vesicula veliger 14 days after hatching. Scale bar = 35 μm. Legend: ldg, left digestive gland; n, nephrocyst; rm, retractor muscle; s, stomach; sgl, shell growth line; st, statocyst.

Figure 2

Haminoea vesicula juvenile approximately 12 days after metamorphosis. Scale bar = 20 μm. Legend: clb, cephalic lobe bud; dgl, digestive gland; e, eye; f, foot; gz, gizzard; mp, mantle pigment; sgl, salivary gland.

dish, etc. These veligers were placed, either individually or in groups of up to 100, in culture chambers containing one or a combination of potentially inducing substrata, all of which were freshly collected from the adult habitat. Substrata used were adult *Haminoea vesicula, Zostera marina, Ulva* sp., surface sediment, and culture dishes with bacterial film. Cultures were maintained at 12–15°C, and were either cleaned and observed daily, or were left undisturbed for 2–5 days. Cultures were maintained until metamorphosis had occurred, or until all veligers had died.

Small juveniles were maintained in 60 × 15-mm Pyrex dishes, then transferred to Tripour beakers with 542-μm mesh vents, both kept at 12–15°C. Juveniles were fed *Zostera marina, Ulva* sp., and bacterial film.

Observations

Ribbonlike egg masses (HURST's, 1967, type A) were attached in a "C" shape to any solid substratum. A typical mass was 36 × 5 × 1 mm in size (as produced by a 42-mm adult) and contained a mean of 76.50 eggs/mm^2 egg mass (±33.68, n = 30 egg masses), for a total of 4000 to 60,000 eggs/mass.

The yellow eggs measured 90.00 ± 3.00 μm in diameter (n = 15), and occurred singly per capsule. Development was synchronous within each egg mass (CHAFFEE & STRATHMANN, 1984). Veligers began to hatch approximately 9 days after oviposition (12–15°C) with shells approximately 120 μm in length. In the laboratory, veligers remained planktonic for approximately 30 days, during which time they grew to a shell length of approximately 180 μm. The major developmental events from oviposition to metamorphic competence are summarized in Table 1. Figure 1 shows a veliger 14 days after hatching. Note the prominent nephrocyst, larval gut including ventral growth of the left digestive diverticulum, and growth lines in the shell.

We had little success in identifying metamorphosis-inducing substrata for *Haminoea vesicula.* However, metamorphosis occurred in some veligers maintained under the following conditions: competent veligers were placed in 500-mL Pyrex beakers containing a 5-day growth of primary film, *Zostera marina,* and an adult *H. vesicula. Isochrysis galbana* and *Pavlova lutheri* were included as food. Cultures were left undisturbed at ambient temperatures for 4–5 days, then searched for juveniles and remaining veligers. Experiments involving only one or two of the above substrata were unsuccessful. Metamorphosis oc-

curred only when all three substrata were present and the cultures were left undisturbed for several days.

All juveniles that metamorphosed in the laboratory had already begun feeding and growth by the first observation (up to 5 days post-metamorphosis). At this time, the buccal mass, radula, salivary glands, and gizzard plates were visible and functional, and the digestive gland was darkly pigmented. The velar lobes had been resorbed, and the foot flattened to project under the head and posteriorly along the shell aperture. As in other cephalaspideans, post-metamorphic shell growth was heterostrophic and involved centrifugal flaring of the aperture until the elongate shell shape of the adult was achieved. Approximately 12 days after metamorphosis, *Haminoea vesicula* juveniles showed the beginnings of the pallial lobes both anteriorly and posteriorly of the shell, mantle pigment, and the adult orientation of the shell (Figure 2). Two cephalic lobe buds were also present, which fused into one as they grew posteriorly. Juveniles were epiphyte and particle grazers, as were the adults. Juveniles were maintained in the laboratory for 250 days, during which time they grew to a mean length of 9.80 ± 1.63 mm (n = 8).

Conclusion

Haminoea vesicula has a pattern of development typical of that of planktotrophic opisthobranchs (THOMPSON, 1967, 1976), and in particular, is similar to *H. solitaria* Say (HARRIGAN & ALKON, 1978). The nature of the metamorphic inducer(s) is not clear, but it appears that at least a primary film is required as a substratum (as in *H. solitaria*; HARRIGAN & ALKON, 1978) in combination with a period during which the competent veligers are left undisturbed.

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Atlantic Records of *Glossodoris sedna* (Gastropoda: Nudibranchia): A Correction

by
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St. Petersburg, Florida 33701, USA

BERTSCH (1988) documented the first western Atlantic records of the nudibranch *Glossodoris sedna* (Marcus & Marcus, 1967), a species previously known only from the tropical eastern Pacific Ocean. The western Atlantic records were based upon two specimens from Tavernier Key and photographs of specimens from Key Largo and "Biscayne Bay," all locations in south Florida.

I provided the photograph upon which the Biscayne Bay record was based, but that location is incorrect. The specimen of *Glossodoris sedna* in my photograph was one of four specimens that I collected in the northeastern Bahama Islands during 3–9 May 1978. The specimens were found together among gorgonian octocorals and algae on rocks in depths less than 1 m near an islet (26°49′N, 77°20′W) immediately north of Green Turtle Cay, Great Abaco.

BERTSCH (1988:398) found it curious that *Glossodoris sedna* was recorded only from localities within 75 km of each other in south Florida and not from other localities in the Caribbean. The record here corrected to the Bahama Islands (approximately 350 km from south Florida) suggests that *G. sedna* may occur elsewhere in the northern Caribbean region.

The four Bahamian specimens of *Glossodoris sedna* are preserved in alcohol (catalogue number FSBC I 32677) in the Marine Invertebrate Collection of the State of Florida Marine Research Institute at St. Petersburg.

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BERTSCH, H. 1988. Anatomy and zoogeography of *Glossodoris sedna* and *Chromodoris grahami* (Opisthobranchia: Nudibranchia) in the tropical western Atlantic and Caribbean. Veliger 30(4):395–399.

The Anthony D'Attilio Student Research Grant in Malacology

The San Diego Shell Club has announced a one-time single research grant of $1000 through the Anthony D'Attilio Grant.

The successful applicant must be in a formal graduate degree program in a U.S. academic institution and the thesis or dissertation topic must further knowledge of the systematics of the Mollusca. The topic may involve research on marine, land, or freshwater mollusks worldwide.

The following documents are required for each application: (1) A proposal, limited to three pages, that discusses the research project and details the work to be aided by this grant and its malacological significance; (2) A budget that outlines how these funds will be used; (3) A curriculum vita or resume; (4) A letter of recommendation from the applicant's thesis advisor; (5) A list of grants and amounts that are currently being received or are anticipated to be received in the 1990–1991 academic year; and (6) An overview of the research project to be sent or presented to the San Diego Shell Club on completion of the project.

The funds are available for the purchase of research materials, usage fees (electron microscope and computer), and travel costs to museums or institutions having resources vital to the research topic.

Completed applications must be received no later than 1 December 1989. Please send to:

Anthony D'Attilio Grant
San Diego Shell Club
3883 Mt. Blackburn Ave.
San Diego, California 92111, USA

For further information, contact Carole Hertz (619) 277-6259.

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a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

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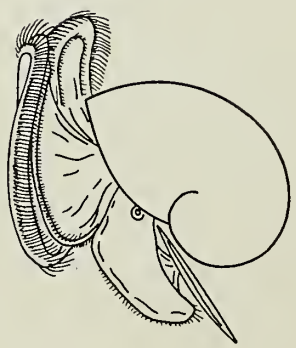

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